EARLY DEVONIAN ECHINODERMS FROM SOUTH AFRICA

PETER A. JELL AND JOHANNES N. THERON

Jell, P.A. & Theron, J.N., 1999 06 30: Early Devonian echinoderms from South Africa. *Memoirs of the Queensland Museum* **43**(1): 115-199. Brisbane. ISSN 0079-8835.

Echinoderms of the Lower Devonian Bokkeveld Group in the Cape Province, South Africa, have played an important role in sedimentary studies of the region but their taxonomic status has been known from only a few cursory papers. We here provide taxonomic treatment of all available crinoid (15 species), asterozoan (11) and blastoid (2) species revising all previously described taxa and more than doubling the known diversity. Palaeobiogeographic affinities appear to be with Europe and the USA but known faunas of South America and Australia are small and almost certainly incompletely known. New taxa described are the crinoid genera *Mandelacrinus nelsoni*, *Eckidocrinus interbrachiatus*, *Sacrinus gamkaensis*, *S. hexensis*, *Monaldicrinus johni* and *Othozecrinus royi* and the asterozoan genera *Aulacolatiaster breviramus* and *Hotchkissaster macrodentatus*. *Hexuraster* is introduced as a replacement for preoccupied *Hexura* Spencer. New species are the crinoids *Kopficrinus halbichi*, *Cradeocrinus plenarius* and *Thalamocrinus arenaceus* and the asterozoans *Marginura hilleri* and *Eugasterella africana*. ❒ *South Africa, crinoids, starfish, ophiuroids, Early Devonian, Bokkeveld.*

Peter A. Jell, Queensland Museum, P.O. Box 3300, South Brisbane 4101, Australia; Johannes N. Theron, Geological Survey of South Africa, P.O. Box 572, Bellville 7530, South Africa; 20 September, 1998.

Echinoderms were first recorded from the Lower Devonian Bokkeveld Group of South Africa as early as 1816 by Dr G. Thom, a clergyman by occupation but also an ardent amateur fossil collector. He gathered 'endless numbers of specimens of shells, trilobites and encrinites or stone lilies'(Thom, 1830). Thus crinoids were the first echinoderms described (Salter, 1856). The Devonian age for the Bokkeveld fossils was assigned about the same time (Sandberger, 1852; Sharpe & Salter, 1856) but in the second half of the 19th century very little was attempted on the identification of these fossils. Rogers and Schwarz mapped these rocks in detail beginning in 1895 and assembled extensive fossil collections that formed the subject of numerous studies illuminating the fossil distribution and stratigraphical setting. Their Devonian age was also confirmed by comparison with faunas from South America and Europe (Corstorphine, 1897; Schwarz, 1906; Reed, 1904, 1906; Knod, 1908; Clarke, 1913; Kozlowski, 1923). In a comprehensive review of the Bokkeveld fauna, Reed (1925) recorded the first carpoid, blastoid and starfish. Echinoderms comprise only a minor element in the fauna however, and detailed descriptions of the various echinoderms in several collections have been rare. Ophiuroids have been mentioned by Rossouw (1933), Spencer (1930, 1950a) and Rilett (1971). Rennie (1936) described carpoids from Gamkapoort, Breimer & Macurda (1972) described blastoids from the Ceres/De Doorns area and Ruta & Theron (1997) described carpoids in detail. In this paper we have revised the description and in many cases the assignment of previously described echinoderms (crinoids, blastoids and asterozoans) and have described substantial new collections from the South African Museum, the Geological Survey of South Africa (mainly collected by J.N.T. during stratigraphic field mapping during the 1970s to 1990s) and the private collection of Mr Roy Oosthuizen of Klaarstroom.

STRATIGRAPHIC SETTING

The clastic Cape Supergroup borders the southern and western parts of South Africa for 800km eastwards and almost 300km northwards from Cape Town (Fig. 1). The Supergroup is divided into a lower, predominantly arenitic Table Mountain Group, conformably overlain by the markedly argillaceous Bokkeveld Group, which in turn is overlain by the more arenitic Witteberg Group (Fig. 2).

The Bokkeveld Group consists of a cyclical alternation of predominantly argillaceous and arenaceous units. Each of these extensive lithostratigraphic units is given formation status (Fig. 2). The 6 lower formations which can be traced

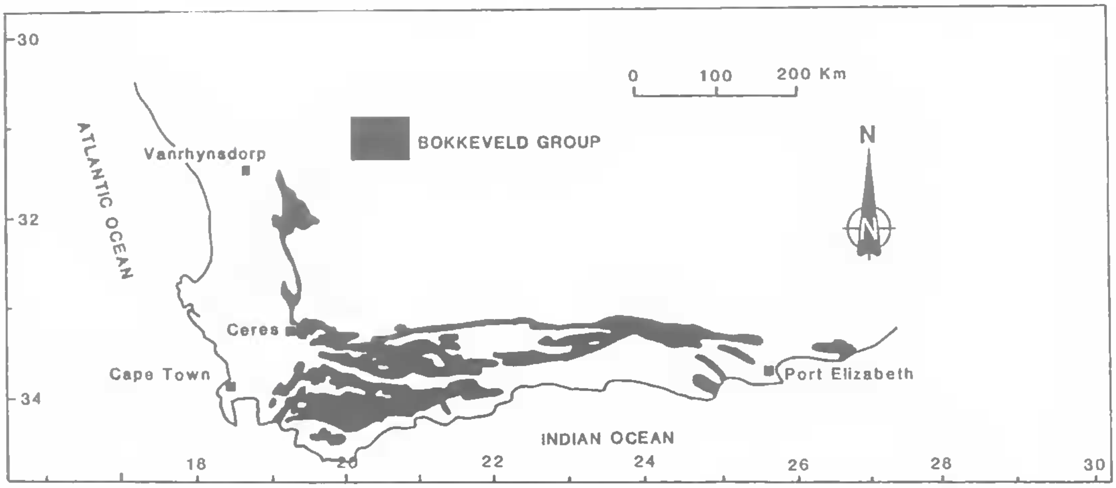


FIG. 1. Sketch map of South Africa showing outcrop areas of the Bokkeveld Group in solid black.

throughout the outcrop area are collectively referred to as the Ceres Subgroup. The upper part of the sequence in the west, with 5 formations, is designated the Bidouw Subgroup, whilst eastwards the laterally equivalent Taka Subgroup consists of 3 formations (Theron, 1972; Theron & Johnson, 1991). Thickness of the Bokkeveld Group is much greater in the east than in the west.

These alternating lithostratigraphic units represent 5 major, sheet-like, superimposed, coarsening-upward cycles which feather out southwards into a relatively homogeneous mudstone-siltstone sequence. This southward decrease of coarser clastics is linked to a progressive thickening of the argillaceous units and of the Bokkeveld Group. The arenaceous units vary from fine-grained quartz arenites to immature arkosic arenites, either horizontally laminated or planar to trough cross-bedded. Hummocky cross stratification becomes a prominent structure northwards (Theron et al., 1995). The argillaceous units consist of dark grey shale, mudstone and siltstone with thin intercalated lenses of fine to medium grained lithic sandstone. The latter reveal swaley cross-stratification and often marked ripple cross laminated zones towards the north.

Weathering of the sequence gives rise to hogback topography, the more resistant arenites creating ridges whereas the intervening argillites generally weather predominantly recessively. This distinctive weathering minimises good exposures of the argillites.

Although numerous fossils have been collected and described, little attention has been paid to their stratigraphic occurrence so that for many years there was no clarity as to whether any zonal scheme could be developed. The faunas vary at a gross level with geography (Schwarz, 1906; Theron, 1972; Oosthuizen, 1984) in that brachiopods and echinoderms are more common in the west, with conulariids, corals and hyoliths more prevalent towards the east.

Usually, marine invertebrate faunas are most common in the Ceres Subgroup, but are found up to the level of the Karoopoort Formation in the west and the Karies Formation in the east (Fig. 2). Although present throughout the Bokkeveld Group, plant and especially trace fossils, become abundant in the northwestern outcrop areas. A wide variety of typically shallow marine ichnogenera occur with large numbers of a variety of the uncommon pentameral stellate trace fossil *Asteriacites* (Fig. 3) at various horizons within these proximal arenites (Theron, 1972).

Examination of sediment/phyla associations reveals distinct affinities of certain species for a particular lithology (Reed, 1907; Theron, 1972; Oosthuizen, 1984). Since a large percentage of the Bokkeveld fauna is benthic organisms, they are likely to be facies controlled. Trilobites and cephalopods tend to occur mainly in argillaceous horizons in contrast to the gastropods, bivalves, and brachiopods which are found more evenly in arenites and argillites. Among echinoderms, the crinoids are found in a variety of sediment types from mudstones to lithic arenites. Although stem fragments are prolific, well-preserved crowns are largely confined to finer grained sediments. Although scarce, ophiuroids, carpoids and

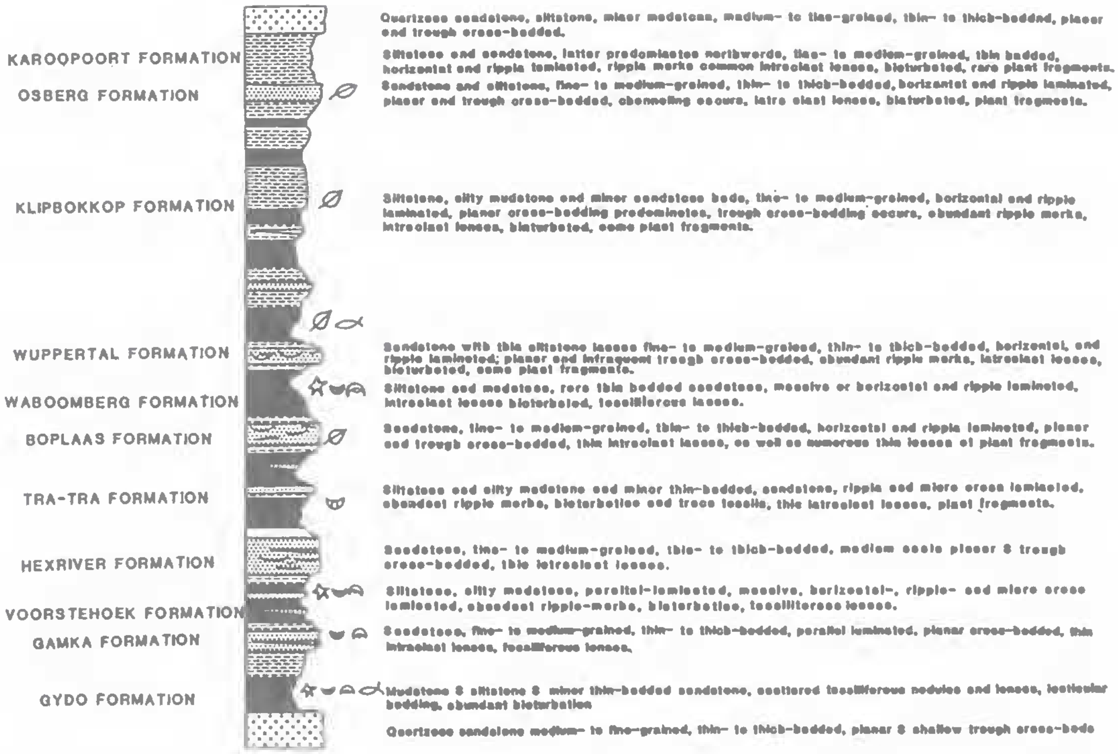


FIG. 2. Stratigraphic section of South African Devonian. The coarse sandstones at top and bottom of section are contiguous parts of the Wittcberg (C3) and Table Mountain (C1) Groups, respectively and indicate upper and lower margins of the Bokkeveld Group (C2). All sediments are siliciclastics; solid black = mudstone, horizontal dashes = siltstone and close dots = fine sandstone. Fossil content is indicated by: star = echinoderms; convex down symbol = shells; convex up symbol = trilobites; two curved lines crossing towards righthand end = fish; leaf shaped symbol = plant fragments. A shorthand nomenclature to reflect cyclicity within the Bokkeveld Group has emerged so that the shales (S) alternate with the sandstones (Q)and are numbered from the base up; thus the Gydo Formation is C2S1, the Gamka Formation is C2Q1, the Voorstehoek Formation is C2S2, etc.

blastoids are similarly found mainly in mudstones, shales or silty shales.

Faunal community structures are recognised (Boucot, 1971; Hiller & Theron, 1988). The overall decrease of Bokkeveld invertebrates and increase in plant fragments and ichnofossils to the north as the argillaceous units become sandier, suggests a shallowing of the basin in that direction. There is a corresponding decrease in fossil content in a southerly direction approaching the deep basin (Theron, 1970, 1972; Theron & Loock, 1988).

PALAEOGEOGRAPHICAL SETTING

The conspicuous change from a few thousand metres of supermature sand (Table Mountain Group) to the predominantly muddy sediments of the Bokkeveld Group throughout the Cape Basin in the Early Devonian, is interpreted as an overall northward advance of the shoreline and progression of shelf and delta slope sediments (Gydo Formation) across the sand-shoal Rietvlei Formation. The latter constituting the uppermost unit of the Table Mountain Group, was deposited in a wide shallow embayment open to the southeast and flanked by a mature low gradient coastal plain (Rust, 1973).

The Bokkeveld sequence reflects the most dynamic phase of the Cape Basin development, when, at the Pragian-Emsian transition, tectonic activity and accelerated downwarping evolved. Pulsatory cyclicity in the vertical stacking of the upward coarsening sequences implies tectonically controlled regressions and transgressions (Theron, 1972; Tankard & Barwis, 1982). These major cycles represent the progradation of lobate wave-dominated deltas along a coastline of moderately high marine energy (Tankard &

FIG. 3. *Asteriacites* sp. A, assemblage of 10 or more complete or partial individual traces in close proximity. T1451 from Vanrhynsdorp (C282), x1.2. (Photo courtesy of John Almond).

Barwis, 1982; Theron & Loock, 1988). Nearshore deposits grade southward into thick shelf mudstones, with the greater thickness towards the eastern Cape reflecting increased downwarping in that direction.

An idealised Bokkeveld genetic sequence consists of sediments laid down successively in the shelf, delta slope and delta platform environments during the constructional phase of delta growth. This is in turn overlain by nearshore marine reworked deltaic deposits, which represent the sediments that evolved during the destructional phase of delta development (Tankard & Barwis, 1982). Storm activity is well-documented in the delta platform sediments, which represent the distributary mouth bar, interdistributary bay and tidal flat deposits, especially in the northern Bokkeveld facies (Theron et al., 1995). Fossils are generally sparse in these sand-, silt-, and mudstones, but occasionally occur as relatively thick lenticular coquinites. Fossils are also generally sparse in the reworked sands of the delta platform. Wave and tidal activity created interspersed barrier washover sheets and tidal inlet and channel fill sequences that were not very conducive to the preservation of fossils.

On the other hand the dark grey mud and siltstones of the Bokkeveld Group contain a rich invertebrate fauna, especially brachiopods and bivalves, which are preserved as scattered internal and external moulds. Coquinites, where present, are relatively thin but laterally persistent; as water depth increased coquinites became rarer. Ebbing storm surge currents entrained shells and sediment from the seafloor and carried them seawards, to where hollows and storm-generated channels acted as traps in which shells and disarticulated crinoidal material accumulated (Hiller & Theron, 1988).

Generally, post-mortem transport of fossils was limited as indicated by the minimal

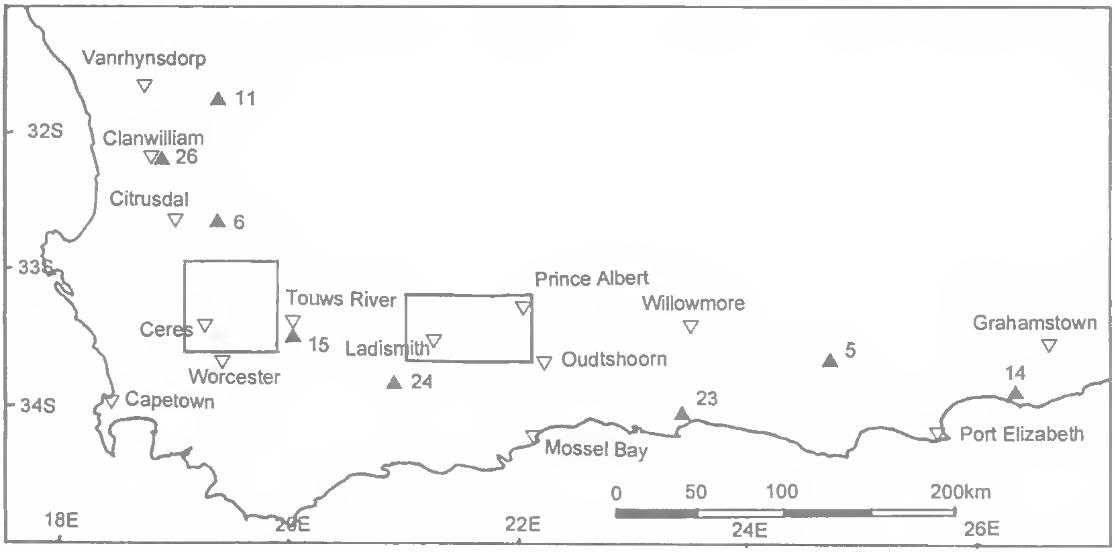


FIG. 4. Sketch map of South Africa indicating the localities from which Lower Devonian echinoderms are known. The 2 frames around the Ceres and Ladismith-Prince Albert districts are enlarged in Figs 5 and 6, respectively. Key to numbered localities outside the frames: 5 = Bucklands; 6 = Grootrivierhoogte; 11 = Platfontein; 14 = Kaaba/Alexandria; 15 = Nouga/Vredefort; 23 = Keurboomstrand; 24 = Warmwaterberg; 26 = Clanwilliam.

mechanical damage to shells. Disarticulated shells are common but rarely display evidence of abrasion or breakage. Furthermore the vulnerability of the multiplated echinoderm skeletons to post-mortem disaggregation generally make preservation of whole crowns relatively rare. In the Gydo and Waboomberg Formations preservation of echinoderms still in life position, indicates predominantly gentle currents and sudden burial, perhaps by smothering mud clouds. Sudden influxes of fine sediment may have come either from the rivers feeding the deltas, or as a result of a storm generating a blanket of wave-stirred mud (Theron, 1972; Hiller & Theron, 1988). This environmental scenario is supported by high concentrations of brittle stars (adult as well as immature individuals), constituting lenticular 'starfish beds' in the Waboomberg mudstones in association with large numbers of infaunal bivalves preserved at a high angle to bedding with their umbones pointing upwards. Co-occurring fenestellid bryozoans, all with the apices of their cones directed upwards suggest overturning by gentle currents. In locally overlying beds well-preserved carpoids are associated with an ostracod fauna and with exquisitely preserved *Lingula,* which are not in life position (Ruta & Theron, 1997; Becker et al., 1994). The frequency of asterozoan trace fossils in the northern proximal shallow marine beds substantiate the original abundance of starfish and brittle stars in the marginal Bokkeveld seas. The relative rarity of asterozoan body fossils in the Bokkeveld sequence is therefore a reflection of the disintegration of their complex skeletons after death. Both ophiuroids and asteroids probably constituted quite an important component of the normal prevalent benthic marine biota of the Bokkeveld Group.

Available data allow correlation (Boucot, 1971; Hiller & Theron, 1988) of several benthic invertebrate fossil communities with various depositional subenvironments in a delta complex: 1, a tidal flat community dominated by inarticulate brachiopods and infaunal bivalves inhabited the sheltered, back-barrier environment; 2, the distributary mouth bar community dominated by brachiopods, occupied the relatively turbulent shallow water setting at the seaward edge of the delta platform; 3, the delta slope community was of intermediate aspect, dominated by brachiopods but more diverse with infaunal bivalves, gastropods, crinoids, cricoconariids and especially trilobites; 4, the shelf community, which although still dominated by brachiopods, is the most diverse community; brachiopods constitute <1/2 the diversity of the assemblage, with trilobites, bivalves and gastropods well represented and echinoderms,

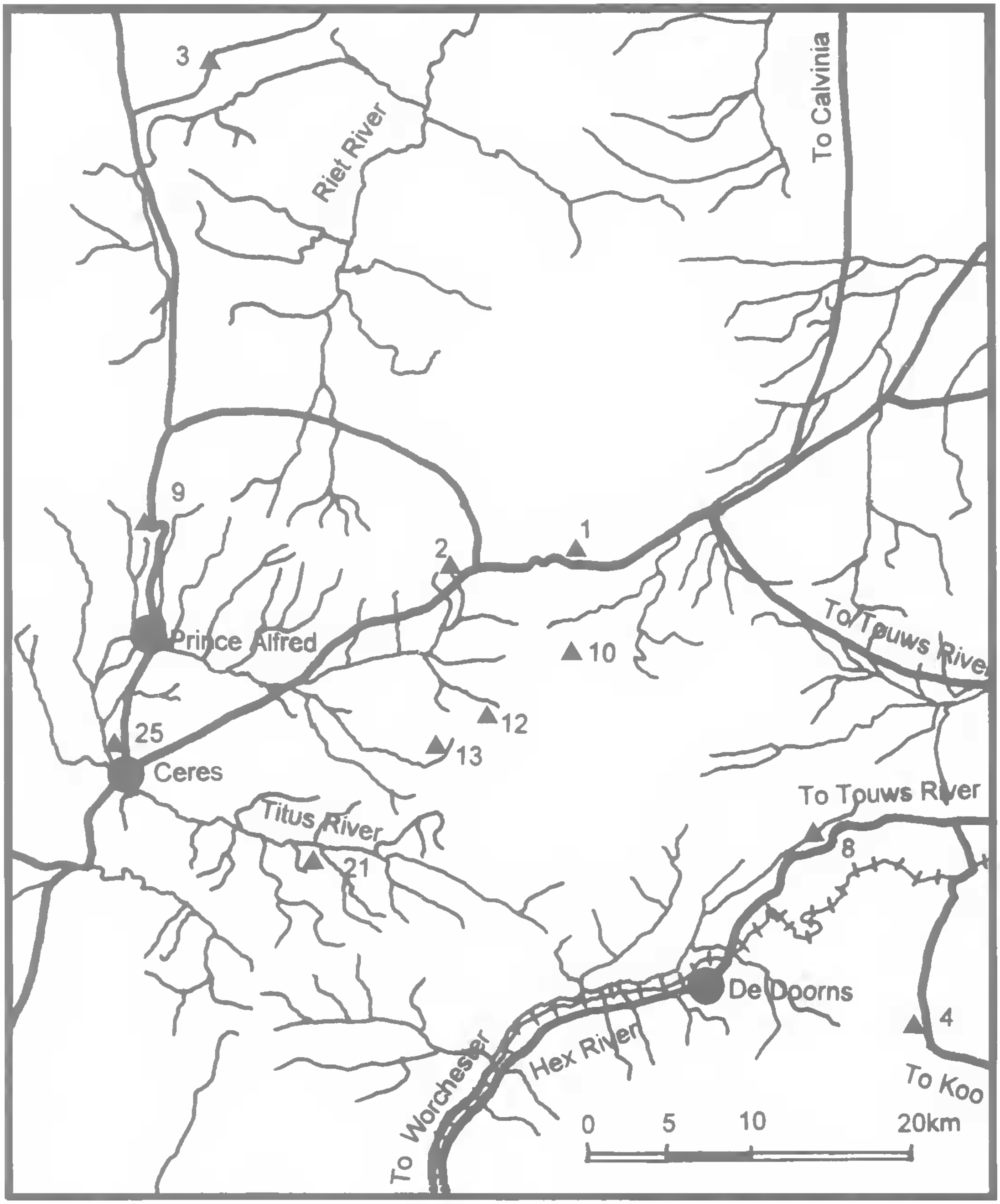


FIG. 5. More detailed locality map of Ceres district as outlined by lefthand frame in Fig. 4. 1=Hottentotskloof; 2=Theronsberg Pass; 3=Tafelberg/Boplaas; 4=Matroosberg/Vredelus; 8=Hex River Pass; 9=Gydo Pass; 10=Die Vlakte; 12=Klipfontein/Lakenvlei; 13=Swaarmoed; 21=Eselfontein; 25=Ceres. Thick black lines are roads; thin crossed line (lower right) is a railway; thin black lines are streams.

hyolithids, corals, bryozoans, conulariids and cephalopods comprising a significant proportion.

In the Gydo and Gamka Formations, which constitute the oldest deltaic cycle, these communities are well-represented. Shelf and

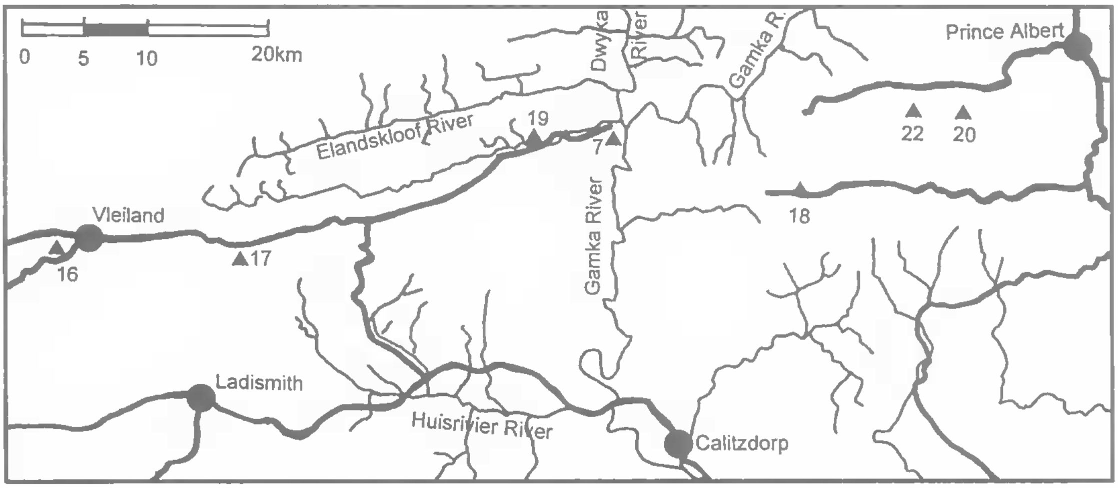


FIG. 6. More detailed locality map of Prince Albert-Ladismith districts as outlined by righthand frame in Fig. 4. 7 = Gamkapoort Dam; 16 = Vleiland; 17 = Koudeveld; 18 = Gamkaskloof; 19 = Bosluiskloof; 20 = Damascus; 22 = Vrischgewaagd. Thick black lines are roads; thin black lines are streams.

slope communities are found in the Voorstehoek Formation and in western outcrops of the Waboomberg Formation, shelf community assemblages have been identified as well. In many of the other formations, available collections are generally too small for community analysis (Hiller & Theron, 1988).

FAUNAL AFFINITIES

All Bokkeveld echinoderm specimens known to the authors were included in the present study. Affinities of the taxa identified (Table 1) are highly equivocal. One bias in this assessment is the variation in levels of knowledge from other parts of the world. The fauna of North America is the best known and in general, most recently studied; in Europe comparably large faunas are known but many have not been given a modern taxonomic treatment; South America and Australia have faunas of this age but they are poorly known (e.g. Australian crinoids (Jell, 1999) as demonstrated in this volume). Early Devonian echinoderms from other parts of the world are virtually unknown and not able to be compared. At species level the South African fauna has a crinoid and an asterozoan in common

TABLE 1. Faunal affinities of the South African echinoderms dealt with herein compared with Europe (1), North America (2), South America (3) and Australia (4). G = the genus occurs in that continent; cf G = a closely related genus occurs in common; S = the species also occurs in that continent; and F = the family is in common.

CRINOIDS	1	2	3	4
Ophiocrinus stangeri Salter, 1856		G		G
Ophiocrinus sp. cf mariae (Kier, 1952)		cf S		G
Corocrinus imbecillus Schmidt, 1941	S	G		
Mandelacrinus nelsoni gen. et sp. nov.	cf G	cf G		
Monocyclic camerate indet.		cf G		
Arthroacantha? sp.		?G		
Eckidocrinus interbrachiatus gen. et sp. nov				
Kopficrinus halbichi sp. nov.		G		
Monaldicrinus johni gen. et sp. nov	cf G	cf G		
Sacrinus gamkaensis gen. et sp. nov	cf G			
Sacrinus hexensis gen. et sp. nov	cf G			
Cradeocrinus plenarius sp. nov	G	G		
Thalamocrinus arenaceus sp. nov.		G		
Othozecrinus royi gen. et sp. nov		cf G		
ASTEROZOANS				
Aulacolatiaster breviramus gen. et sp. nov.	cf G	cf G		
Ulrichaster macrodentus gen. et sp. nov	G	G		
Haughtonaster reedi Rilett, 1971		cf G	cf G	
Hexuraster weitzi (Spencer, 1950a)	F	F		F
Encrinaster tischbeinianus (Roemer, 1862)	S			
Marginura hilleri sp. nov.			G	
Eugasterella africana sp. nov.		G		
Stratasteer ohioensis Kesling & LeVasseur, 1971		S		
Stratasteer stuckenbergi (Rilett, 1971)		G		
BLASTOIDS				
Pachyblastus dicki Breimer & Macurda, 1972			S	
Brachyschisma ootheizeni Breimer & Macurda, 1972		G		

with Europe, a crinoid and an asterozoan with North America and a blastoid in common with South America. At the generic level most matches are with North America, then Europe, then a very few with South America and Australia. The 25 South African echinoderms dealt with herein do not provide a statistically large enough sample to make any compelling arguments and thus the affinities must be considered unknown at this stage. Brachiopod affinities (Boucot et al., 1969) place South Africa in the cool water Malvinokaffric Realm suggesting that further study of South American echinoderms may reveal closer affinities.

SYSTEMATIC PALAEONTOLOGY

The following abbreviations indicate repositories for the material discussed in the text:- British Museum of Natural History (BMNH), Geological Survey of South Africa, Pretoria (PRV), Geological Survey of South Africa, Bellville in Capetown (B), Roy Oosthuizen Collection, Zwartskraal, Prince Albert (RO), South African Museum, Capetown (SAM), Geological Collections, Stellenbosch University, South Africa (SU), Rhodes University, Grahamstown (RUGDNH), Natal Museum, Durban (NM) and Sedgwick Museum, Cambridge University, England (SM A). All illustrations are of latex casts taken from external moulds unless otherwise stated; they are whitened with a sublimate of ammonium chloride for photography.

Class CRINOIDEA Miller, 1821

Terminology follows Moore & Teichert (1978). Measurements are given as: length, parallel to the central axis; width, transverse to, but never cutting or joining the central axis; and depth, normal to, and may join central axis.

Subclass CAMERATA Wachsmuth & Springer, 1881
Order DIPLOBATHRIDA Moore & Laudon, 1943
Superfamily RHODOCRINITOIDEA Roemer, 1855
Family OPSIOCRINIDAE Kier,1952

Although Kier (1958) advocated elimination of the Opsiocrinidae after he recognised that *Opsiocrinus* was dicyclic, Ausich (1986) found the family useful in his classification of the Rhodocrinitoidea. Frest & Strimple (1981) and Ausich (1986) recognised that several of his familial characters are of generic standing in some cases in the same group. With this in mind the classification may be considered preliminary. Frest & Strimple (1981) and Ausich (1986) recognised the cofamilial relationship of *Opsiocrinus* and *Ophiocrinus*; we consider these genera synonyms (see below). We use Ausich's (1986) classification herein but following ICZN Article 40 the family name based on the junior synonym remains valid.

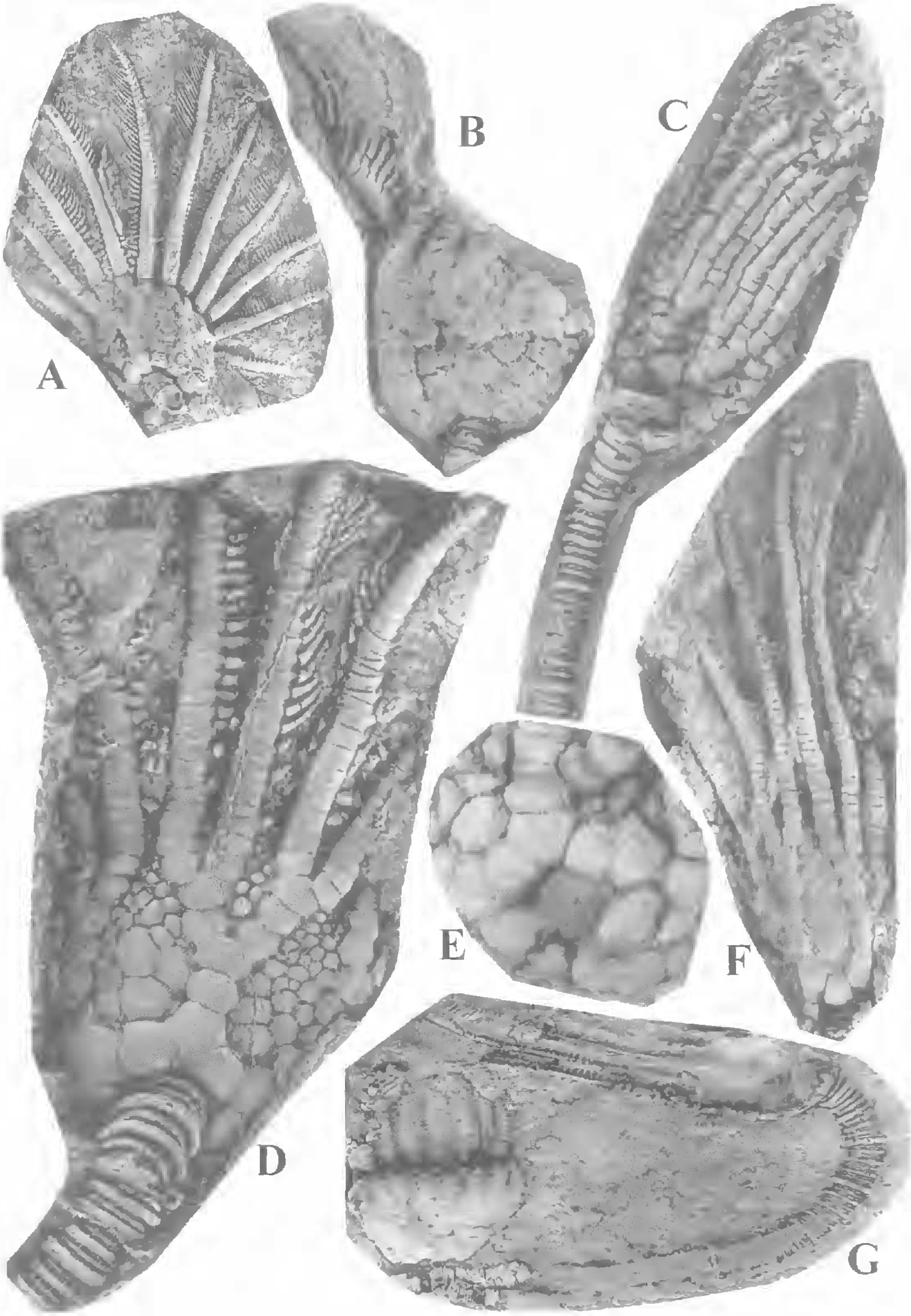
Ophiocrinus Salter, 1856

TYPE SPECIES. *Ophiocrinus stangeri* Salter, 1856 from the Lower Devonian Bokkeveld Series, South Africa; by monotypy.

DIAGNOSIS. Infrabasals 5, forming a pentagon completely or almost completely concealed by stem; interbrachials numerous, depressed, small, regular, especially in proximal part of interrays; CD interray conspicuous, with anitaxis of subquadrate anal plates variously developed in field of small irregular plates on either side. Arms 10 or 20, free and becoming cuneate then biserial distal to last arm division, unbranched distally. Stem circular or pentagonal in section, with narrow marginal crenularium, heteromorphic.

REMARKS. The only significant differences between *Opsiocrinus* Kier, 1952 and *Ophiocrinus* appear to be the number of arms, length of anitaxis and cross section of the stem. Frest & Strimple (1981, table 1) showed that the2 genera

FIG. 7. *Ophiocrinus stangeri* Salter, 1856. A, deformed crown with pinnulate biserial arms, RO39, ×1. B, C-D interray view of crown showing 3 vertical columns of anal plates B4603, ×2. C, small specimen showing uniserial arms well away from theca and biserial arm on left high up, B4544, ×3. D, holotype crown with C-D interray on left, with 1st interprimibrach supporting 4 anal plates, with uniserial brachials proximally gradually becoming cuneate then biserial distally, SM A3441, ×4. E, basal view of small cup showing subpentagonal stem facet, from the Gydo Formation in a quarry on E side of road N from Prince Alfred's Hamlet, 1km S of Gydo, B4670, ×5. F, small deformed crown SAM13479, ×2. G, two crowns compressed in the same direction, that on left with diminished crown length and that on right compressed laterally and showing the infrabasal circlet on top of the stem viewed from inside the cup. SAMK972, ×1.25.


A
B
C
D
E
F
G

are distinguished only by the number of arms and in the nature of arm brachials. Although there is a reversal (clearly a typographical error) between their text and table 1 with *Ophiocrinus* being credited with cuneate brachials in the text but biserial ones in table 1. Regardless of this confusion the larger collection of *O. stangeri*, now available, allows confirmation that the arms in both genera progress distally from rectangular to cuneate to biserial. Length of the anitaxis, with 4 plates in one genus and 2 in the other could well be considered a specific discriminator if consistent (1 CD interray is available for *Ophiocrinus* and 2 for *Opsiocrinus*). Some camerate genera contain species with different numbers of arms. One specimen of *O. stangeri* (Fig. 2C) has a ray with only 2 arms as opposed to the usual 4 in adjacent rays; a 2nd specimen (Fig. 1B) shows the beginnings of the radial interplate ridge patterns so prominent in some *Opsiocrinus mariae* Kier, 1952 (Kesling & Chilman, 1975, frontispiece, pl.40, figs 11-14); several specimens (Fig. 1A, 2A, 3B) have slight, barely visible re-entrants in the proximal margin of the basal plates which probably accomodated the corners of the infrabasal pentagon as in *O. mariae*. This indicates that orientation of the infrabasal pentagon to the basal circlet changed from the exterior to the interior as described by Kier (1958, fig. 1) in *O. mariae* because the interior of the cup in *O. stangeri* (Fig. 3E) shows the infrabasal pentagon with the angles at the sutures between basals and the sutures between infrabasals at the centre of the basals. The stem of the North American species is inferred to be pentagonal because of the shape of the attachment facet on the cup. In *O. stangeri* the stem is round but in at least 1 specimen (Fig. 1G) the attachment facet or the 1st columnal is pentagonal. Thus we synonymise these 2 genera despite their geographic and stratigraphic (Early Devonian vs Middle Devonian) separations. Ausich (1986:87) inferred 2 lineages within the Opsiocrinidae from the Llandovery into the Devonian with the 2 Devonian genera on separate lineages based on cup shape, prominence of ridges and arm numbers. However, cup shape and ridge pattern are identical in the 2 Devonian genera and taking the rudimentary ridge pattern in a specimen of *Ophiocrinus* even the interbrachial ornament may be allied. The relation of the infrabasal circlet to the basal circlet is another feature which seems to join the 2 Devonian genera. Other monophyletic camerate genera are known to have 10 and 20 armed

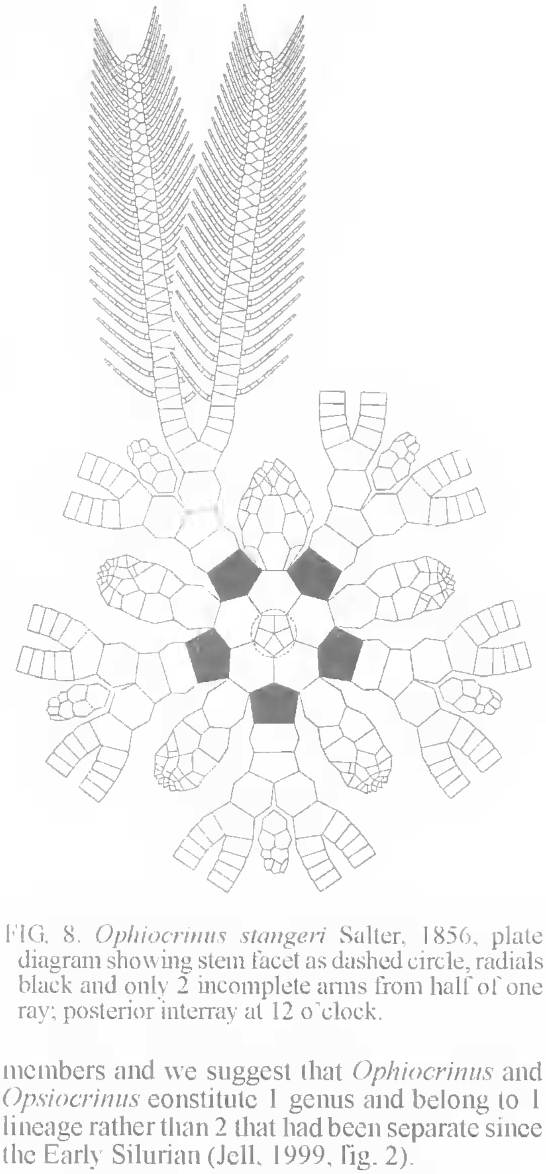


FIG. 8. *Ophiocrinus stangeri* Salter, 1856, plate diagram showing stem facet as dashed circle, radials black and only 2 incomplete arms from half of one ray; posterior interray at 12 o'clock.

members and we suggest that *Ophiocrinus* and *Opsiocrinus* constitute 1 genus and belong to 1 lineage rather than 2 that had been separate since the Early Silurian (Jell, 1999, fig. 2).

Ophiocrinus stangeri Salter, 1856
(Figs 7-10)

Ophiocrinus stangeri Salter, 1856:223, pl.25, fig.20; Ubaghs, 1978: T428, fig. 238.2.

MATERIAL. HOLOTYPE: SMA3441 from De Dooms, Hex Rivier Poort (donated to the Sedgwick Museum, Cambridge in 1932 from the collection of Dr W. Stanger. B4523 from Bucklands, eastern Cape Province(C2S1), B4526-4530 from Gamkapoort Dam (C2S1), B4544, B4553, B4603 from Gydo Pass (C2S1), B4551, B4552 from Gamkapoort Dam (C2S1), RUGDNH1 from Klein Kaaba, Alexandria district, eastern Cape (Voorstehoek Formation), B4579; RO S17, RO S20 from Grootrivier,

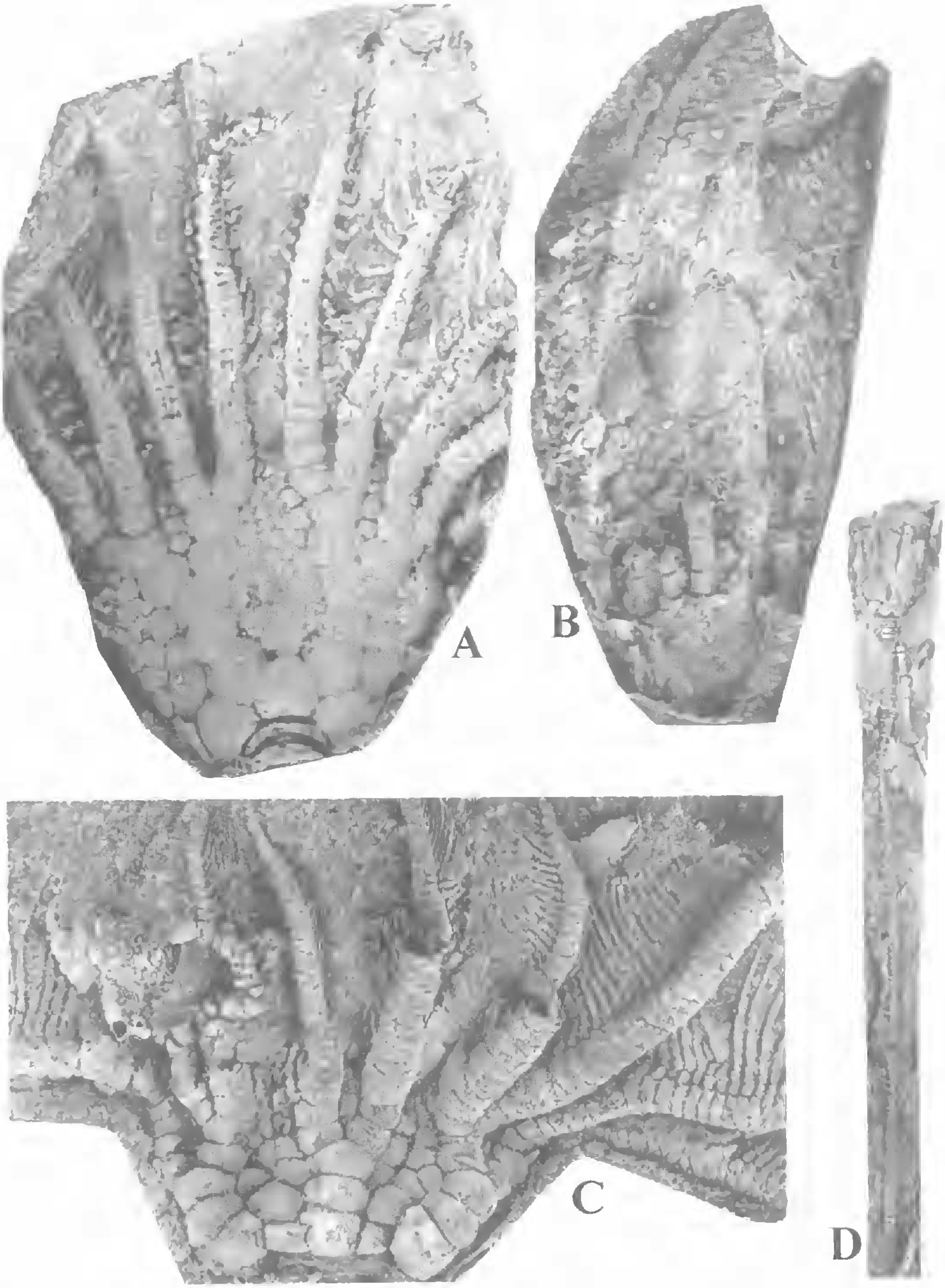


FIG. 9. *Ophiocrinus stangeri* Salter, 1856. A, crown showing B and C rays, RO S20, ×5. B, small crown with arms on anterior (or A ray) side missing to expose anal tube, K4532, ×4. C, large crown showing some normal arms (on right) but mostly arms that have been broken off during life and regenerated producing major change in arm diameter, B4553, ×2.5. D, crown on long stem suggesting high level feeder, SAM13459, ×1.

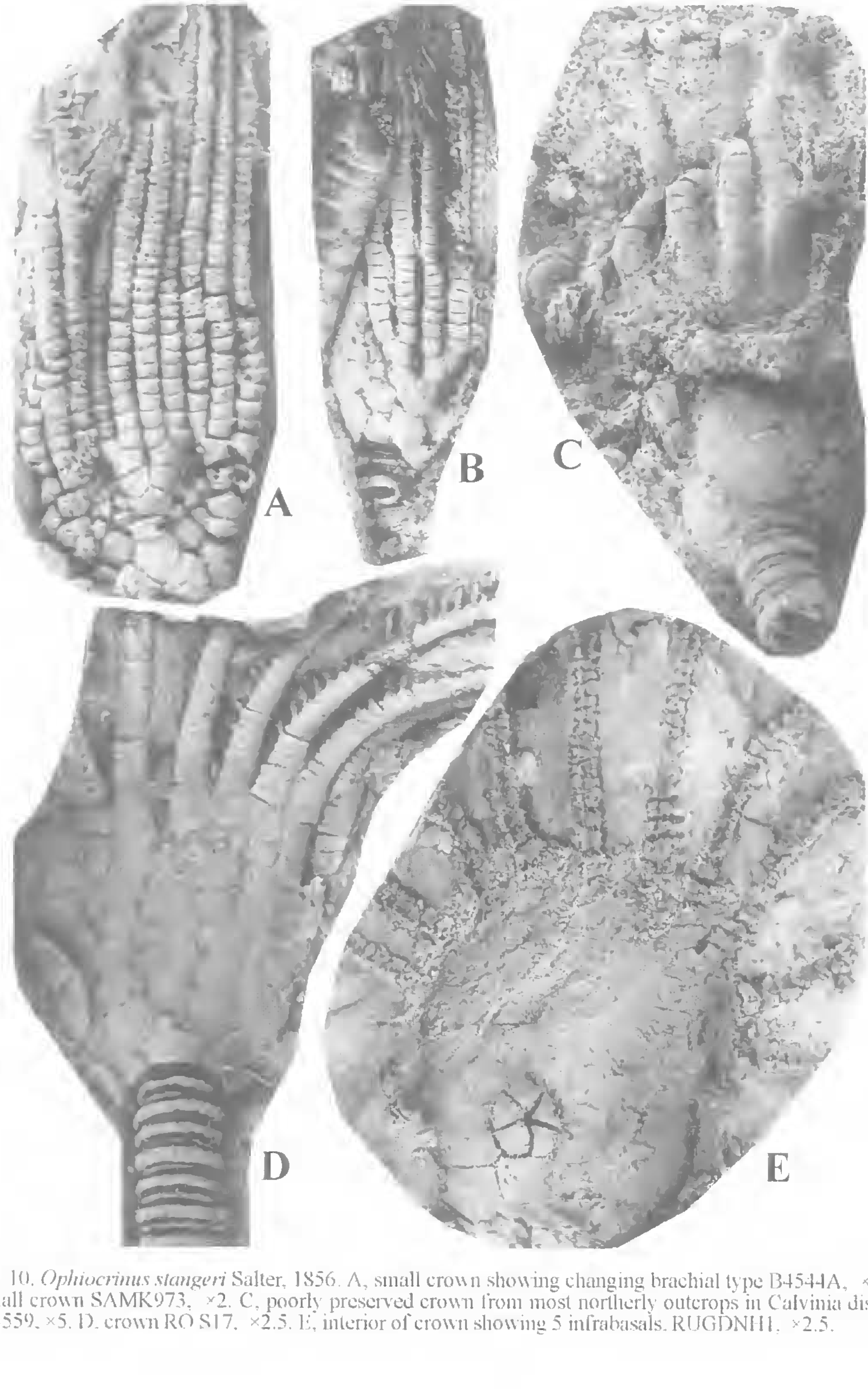


FIG. 10. *Ophiocrinus stangeri* Salter, 1856. A, small crown showing changing brachial type B4544A, ×5. B, small crown SAMK973, ×2. C, poorly preserved crown from most northerly outcrops in Calvinia district, B4559, ×5. D, crown RO S17, ×2.5. E, interior of crown showing 5 infrabasals, RUGDNH1, ×2.5.

Ceres at 32°38'S, 19°24'15"E (C2S1), RO39 from Gamkapoort at 33° 18'S, 21° 38'E (C2S1), SAMK967, 969, 970, 972, 973, 975 from Wolfaardt's Farm, Riet Valley, Ceres, SAM9703 from Clanwilliam, Cape Province, SAM13459 from Boschluis Kloof, SAM13462, 13464, 13479 from Koudeveld Berg, above 2nd sandstone.

DESCRIPTION. Crown up to 60mm long, subcylindrical, with arms about 3 times as long as cup. Cup bowl-shaped, up to 25mm maximum diameter, of moderate length, with smooth plates. Infrabasals 5, small, equal, diamond-shaped, concealed by stem. Basals 5, 7-sided, longer than wide, with greatest width in proximal 1/2, rarely with depressed and weakly isolated lateral tips beneath tips of radial (e.g., in holotype), often with slight re-entrant in proximal side presumably accomodating angle of the infrabasal pentagon. Radials 5, pentagonal, not in contact with other radials, penetrating deeply into basal circlet; radial facet plenary. First primibrach hexagonal, wider than long; 2nd primibrach axillary, pentagonal; secundibrachs 2 or rarely 3, fixed, subquadrate; tertibrachs free, becoming triangular distally. Arms 20 (rarely 18), uniserial proximally, becoming almost biserial distally, pinnulate with pinnules on long side of triangular tertibrachs alternating from side to side on successive plates, with well-developed oral groove. CD interray with 2 large hexagonal plates forming central anal column flanked by smaller polygonal anal plates; primanal hexagonal, in radial circlet, similar in size to radials. Interprimibrachs small, numerous in each ray; proximal 1 septagonal, resting on basals: 2 in second row, 3 in next row, increasing in number and decreasing in size distally; interbrachial field decreasing in width adjacent to secundibrachs as arms spread laterally. Intersecundibrachs in larger specimens, 1 in first row, 2-3 in more distal rows. Tegmen unknown. Stem circular, heteromorphic, noditaxis N212 proximally with nodals longer and of greater diameter than internodals, distally with noditaxis N3231323, with intercolumnal sutures strongly crenulate, greatest length among available specimens 15cm (uniform diameter of 2mm), greatest diameter 4mm.

REMARKS. Among available specimens only the holotype shows the CD interray so we have no data on possible variation in this area of the cup, nor any data on the tegmen which is concealed by the arms. One specimen (Fig. 9B), here tentatively assigned to *O. stangeri*, has a long anal tube, about 1/2 length of arms and covered by small polygonal plates; the tegmen of this common species should be sought in future collecting to confirm this feature. The unbranched, free, pinnulate arms in which the brachials become more and more cuneate distally together with a fragment of stem identical with that of *O. stangeri* lying beside the cup suggest assignment to *O. stangeri*; negative evidence is provided by the lack of any other species with this type of arm in the rest of the South African Bokkeveld crinoids available at present. We make the assignment tentative in the absence of detail of the cup.

Some intraspecific variation is recorded in the description above with other variation: 1, in a few specimens (Fig. 7C, F) the distal noditaxis extends much further proximally i.e. proximal stem resembles distal stem of most specimens; 2, in some specimens, particularly smaller ones (c.7mm cup diameter) proximal tertibrachs are more quadrate than rectangular in lateral view, becoming cuneate distally; 3, intersecundibrachs are not present in these smaller or even some larger specimens; 4, in one specimen (Fig. 7B) the threeway intersections of sutures in the interprimibrach and intersecundibrach areas are depressed, suggesting a subtle interplate ridge system as in *Opsiocrinus*.

At species level this taxon is unmistakeable and distinct from the most similar *O. mariae* Kier,1952 in number of arms, depression and ornament in interbrachial areas and CD interray plating. *O. stangeri* is the most common crinoid in available collections from the Bokkeveld Series but is still incompletely known.

Ophiocrinus sp. cf. **mariae** Kier, 1952
(Fig. 11)

MATERIAL. A cup RO179 from Cockscomb Mountains, Steytlerville, near Bucklands at 33°31'S, 24°44'30"E in the Gydo Formation.

DESCRIPTION. Infrabasal circlet just visible laterally, with sutures between infrabasals directed at midline of basals, angles of infrabasals directed at sutures between basals; strong ray ridges elevated, occupying most of plate width from basals up to at least 2nd secundibrach; 10 arms; interprimibrach series 1-2-3 decreasing in size at level of arm branch, with strong radial ornament of central tubercle and radial lines sometimes consisting of a series of tubercles, with 7 radial ridges on the 1st interprimibrach, with 6 ridges on plates of next row; 1-2 intersecundibrachs with 5-rayed ornament.

REMARKS. This specimen may represent an undescribed species but it resembles *O. mariae* Kier,1952 more than it does the South African *O.*

FIG. 11. *Ophiocrinus* sp. cf. *O. mariae* (Kier,1952) partial cup showing depressed interbrachials with stellate ornament. RO179, ×5.

stangeri: its 10 arms, 2nd primibrach axillary, strongly depressed interbrachial plates with stellate ornament, and strongly depressed 3-way sutural junctions in the cup are features of *O. mariae* but the laterally visible infrabasals, ray ridges standing high on the arm plates and 7-rayed ornament on the 1st interprimibrach differ from that species. It is simply distinguished from *O. stangeri* by its 10 rather than 20 arms and the ornament on the interprimibrachs. Without knowledge of the posterior, stem or higher arms we prefer to make tentative assignment only.

Order MONOBATHRIDA
Moore & Laudon,1943
Suborder COMPSOCRININA Ubaghs,1978
Superfamily PERIECHOCRINOIDEA
Bronn,1849
Family PERIECHOCRINIDAE Bronn,1849

Corocrinus Goldring,1923.

TYPE SPECIES. *Corocrinus ornatus* Goldring,1923 from the Middle Devonian Ludlowville Shale, New York; by original designation.

Corocrinus imbecillus Schmidt,1941
(Figs 12)

Corocrinus imbecillus Schmidt, 1941: 97, pl. 14, figs 3,4.

MATERIAL. HOLOTYPE: E3142 in the Museum für Naturkunde, Berlin, from the Lower Devonian, Upper Koblenz Shale, western Germany. South African material ROC25, ROT17 and B4551 all from Gamkapoort Dam in the Gydo Formation.

DIAGNOSIS. Like type species but with 20 arms.

DESCRIPTION. Cup high conical, up to 20mm maximum diameter, of moderate height; plates with strong radial ornament, with high ray ridges; ray ridges wide on basals, becoming higher relative to the plates and more narrowly arched in section above the axillary primibrach. Basals 3, sutures in B and E rays and CD interray, equal, pentagonal, visible in lateral view, with 3 prominent ridges radiating distally. Radials 5, hexagonal (A,C,D) or heptagonal (B,E), in contact with other radials except in CD interray, slightly longer than wide, with 6 strong radial ridges including ray ridge. First primibrach hexagonal, longer than wide, with 6 radial ridges; 2nd primibrach axillary, pentagonal, with 5 radiating ridges including the Y-shaped ray ridge. Secundibrachs elongate, fixed, with 2nd or 3rd axillary, (most often both axillary in 1 arm but any pattern not available). Tertibrachs free, uniserial, with interbrachial sutures becoming oblique distal to 2nd or 3rd brachial but brachials never triangular. Arms 20, uniserial, strongly pinnulate; pinnules long (up to 1cm long in available specimens), of 8 or more pinnulars, 1 per brachial, alternating from side to side up arm. CD interray wide, with ridge up median line of plates (Fig. 12A); primanal large, heptagonal, in radial circlet, similar in size to radials, supporting 3 hexagonal anals distally. Interprimibrach series elongate, with proximal one hexagonal, resting on 2 radials, supporting 2 smaller hexagonal interprimibrachs in next row, all with 6 radial ridges; more distal rows of smaller plates with central tubercules and radial ridges. Intersecundibrachs numerous, 1 in proximal row, small, centrally tuberculate. Anal sac (Fig. 12C) of many small polygonal abutting plates, about as long as cup, possibly flexible. Stem circular, heteromorphic, with noditaxis of N2I2 pattern; intercolumnal sutures strongly crenulate; greatest length among available specimens 90mm, diameter 3mm proximally, 2mm distally.

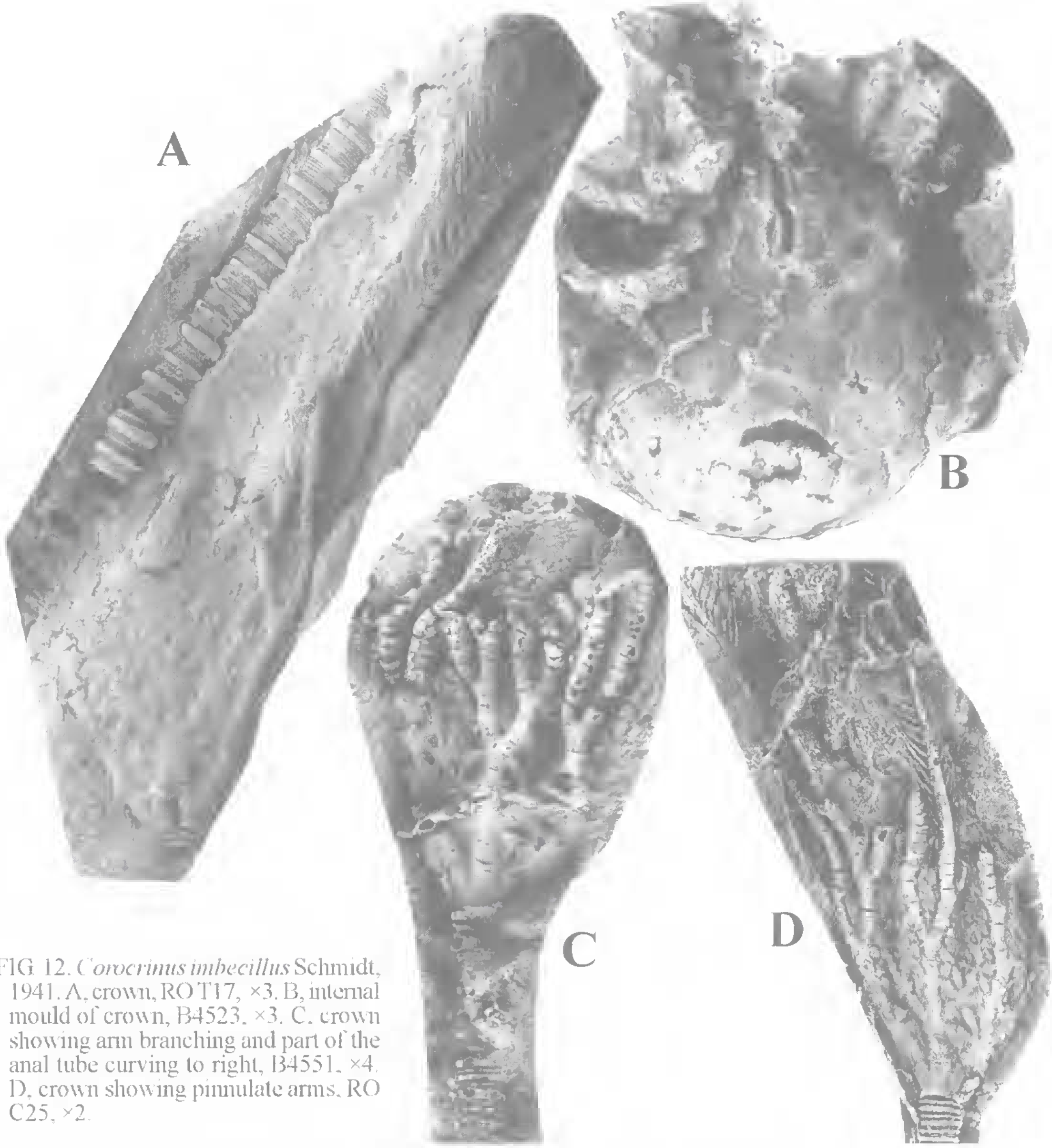


FIG. 12. *Corocrinus imbecillus* Schmidt, 1941. A, crown, RO T17, ×3. B, internal mould of crown, B4523, ×3. C, crown showing arm branching and part of the anal tube curving to right, B4551, ×4. D, crown showing pinnulate arms, RO C25, ×2.

REMARKS. Breimer (1962) noted the close similarity of this species to the type species and we can only make species distinction on the number of arms; none of Goldring's (1923) material of the type species has any free arms attached so that if a further bifurcation occurred in the free arms it would not be available on her material. We therefore, reserve the possibility that *C. ornatus* and *C. imbecillus* could be synonymous. Breimer (1962) placed weight on the axillary primibrach having 7 sides; externally the axillary primibrach of *C. imbecillus* is not clear on Schmidt's (1941) material or on the South African specimens but the internal mould (Fig. 12B) shows the shape of cup plates very well and the axillary primibrach is 7-sided, agreeing with Ubaghs diagnosis.

Mandelacrinus gen. nov.

TYPE SPECIES. *Mandelacrinus nelsoni* sp. nov.

ETYMOLOGY. For Nelson Mandela, President of South Africa.

DIAGNOSIS. Cup low conical; plates smooth, with margins depressed in interadii, with strong wide ray ridges leaving narrow depressed marginal zone on fixed brachials. Basals 3, sutures in B ray, CD interray (and presumably E ray). Radials hexagonal, laterally in contact except in CD interray. First primibrach hexagonal; 2nd primibrach axillary, pentagonal. CD interrary wider than other interrays, primanal interrupting radial circlet, supporting 3 hexagonal anals in 2nd row, 5 in 3rd row, 6 in 4th row at level of 1st secundibrach then diminishing on to tegmen. Interprimibrachs small with central tubercle distal from 3rd row. Intersecundibrachs small, tuberculate. Arms 20, biserial distal to 2nd tertibrach, pinnulate; pinnules long, slender, a row along either side of arm, 1 per brachial. Stem circular, of alternating nodals and internodals proximally.

REMARKS. Three basals, separation of C and D radials by the primanal, other radials in contact and hexagonal 1st primibrach suggest the Periechocrinidae but the single fixed secundibrach is not a feature of that family. However, co-familial *Corocrinus* has only a few fixed secundibrachs and makes a reasonable ancestor for the new genus. The shorter cup, wider interradii, less ornamented cup, biserial arms and single fixed secundibrach may all be considered derived character states relative to *Corocrinus*.

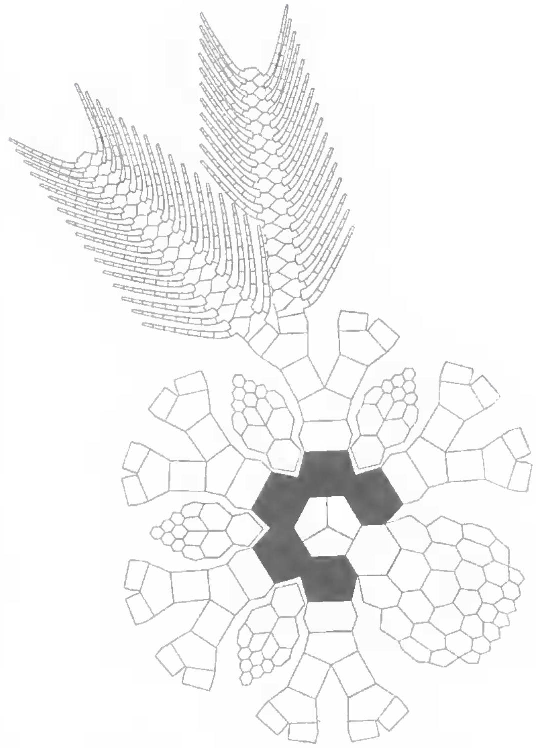


FIG. 13. *Mandelacrinus nelsoni* gen. et sp. nov., sketch of plate arrangement with radials darkened; anterior - posterior axis in NW-SE line; most arms shown as far distally as 1st tertibrachs with distal portions (not including tips) sketched for 2 arms on left of B ray.

Mandelacrinus nelsoni sp. nov.
(Fig. 13, 14)

MATERIAL. HOLOTYPE: RO740 from the Cockscomb Mountains, Steytlerville, near Bucklands at 33°31'S, 24°44'30"E in the Gydo Formation. PARATYPE: SAMK976 from Wolfaardt's Farm, Riet Valley, Ceres..

DIAGNOSIS. As for genus.

DESCRIPTION. Cup 6-13mm long, low conical, up to 15mm diameter; plates smooth, with depressed margins, with well-developed ray ridges standing well above lateral parts of plates particularly about the secundibrach level where arms begin to stand away from cup. Basals 3, sutures in B and E rays and CD interray, equal, pentagonal, visible in lateral view. Radials 5, hexagonal, in contact with other radials except in CD interray, wider than long in holotype, longer than wide in small specimen. First primibrach hexagonal, wider than long; 2nd primibrach axillary, pentagonal; 1st secundibrach fixed, hexagonal, with flat lateral areas rising up strongly to high ray ridge; 2nd secundibrach axillary, pentagonal; tertibrachs free, biserial from 2nd. Arms 20, biserial from 2nd tertibrach, strongly pinnulate; pinnules long (up to 1cm long in smaller specimen), of 7-8 pinnulars, 1 per 1/2 brachial in 2 rows along arm. CD interray wide, with ridge up median line of plates (Fig. 6B); primanal large, heptagonal, in radial circlet, similar in size to radials, supporting 3 hexagonal anals distally, followed by rows of 5 then 6 anal plates, then decreasing in size and number between maximum width of fixed arms. Interprimibrach series narrow, elongate; 1st interprimibrach hexagonal, resting on 2 radials, supporting 2 large hexagonal interprimibrachs distally; 3rd row of 3 small centrally tuberculate plates and 4th row same but with 5 plates. Intersecundibrachs 1 or 3, 1 in proximal row, centrally tuberculate, 2 in distal row. Tegmen unknown. Stem circular, up to 4mm in diameter, heteromorphic proximally becoming uniform distally, noditaxis uncertain but probably N212; intercolumnal sutures strongly crenulate; greatest length available 3cm.

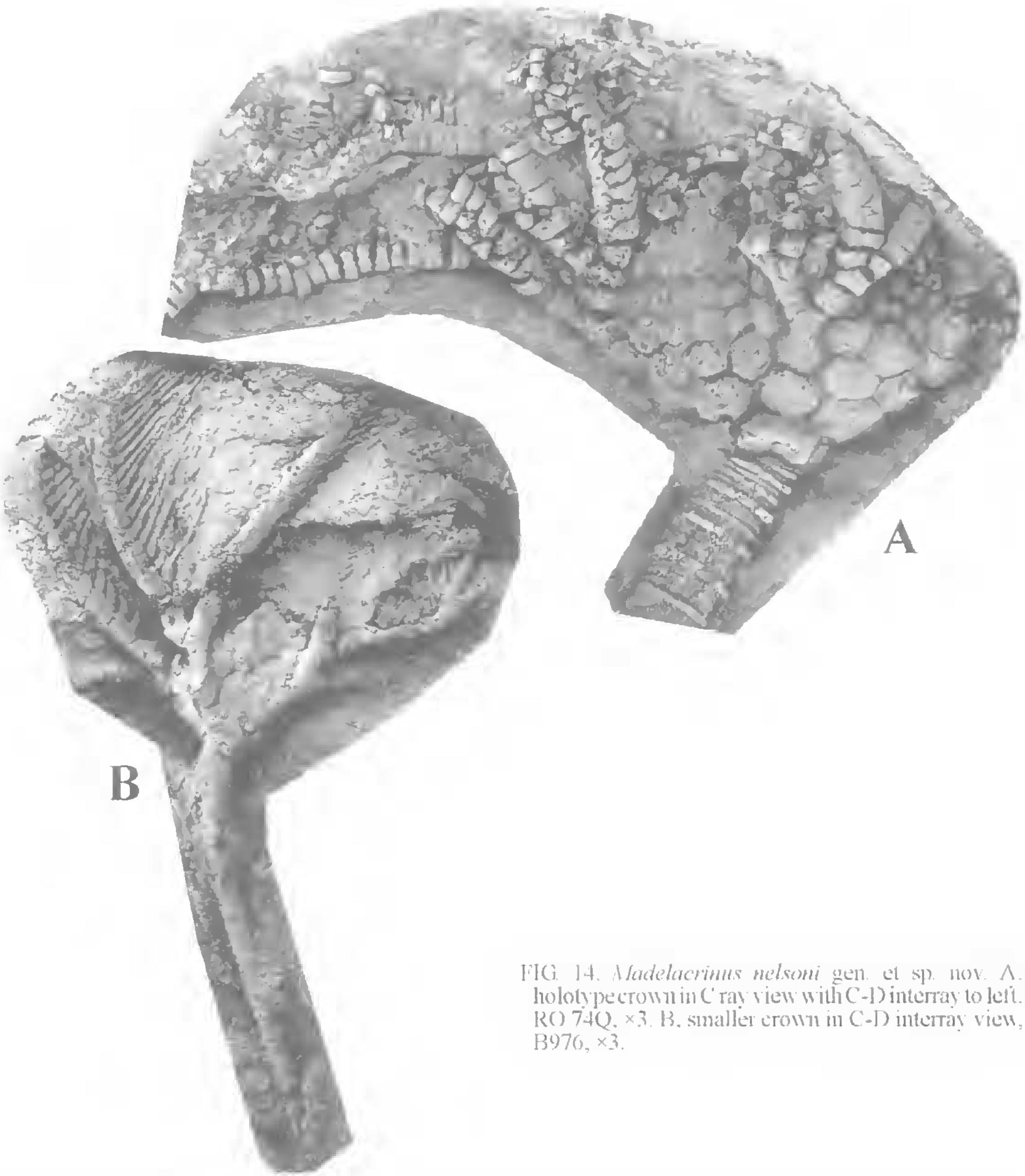


FIG. 14. *Madelacrinus nelsoni* gen. et sp. nov. A, holotype crown in C ray view with C-D interray to left, RO 74Q, ×3. B, smaller crown in C-D interray view, B976, ×3.

REMARKS. Of the 2 specimens 1 is twice the size of the other and both show the posterior of the cup to confirm that they belong to the same species. There do not seem to be any other genera closely comparable as mentioned above.

Monocyclic camerate indet.
(Fig. 15)

MATERIAL. PRV HR-5 from the Hex River area.

DESCRIPTION. Cup probably conical, about 8mm long; plates smooth or with very subtle vermiform ornament. Basals apparently 5, pentagonal. Radials 5, largest plates in cup, 7-sided; 1st primibrach hexagonal; 2nd primibrach axillary; interprimibrachs and intersecundibrachs normal polygonal plates decreasing in size distally. Arms 10, uniserial, of cuneate brachials, highly pinnulate; pinnules

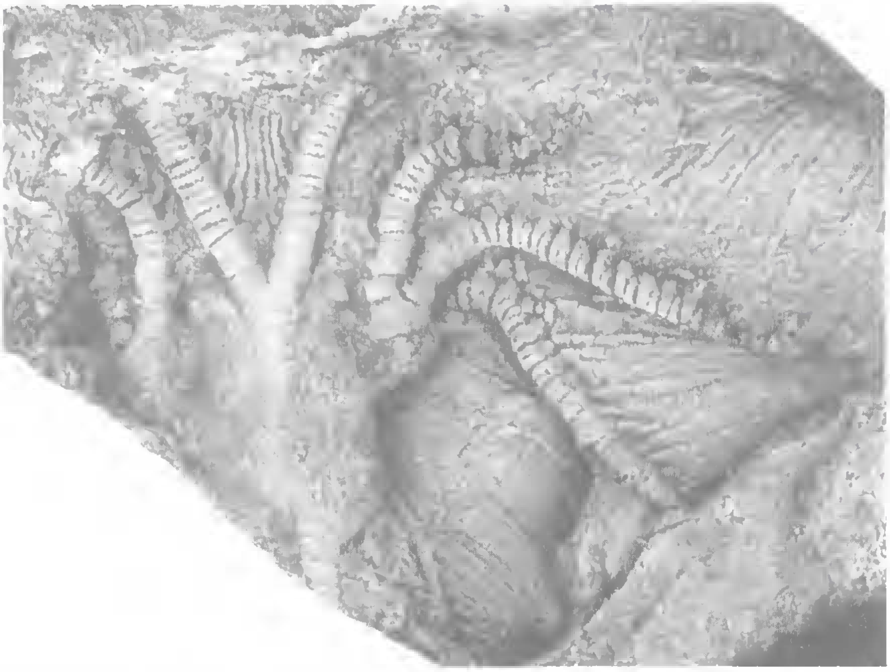


FIG. 15. Monocyclic camerate indet. Crown showing long pinnules and triangular brachials, PRV HR-5, ×4.

alternating from side to side on long side of brachials.

REMARKS. Without details of the posterior it is not possible to classify this specimen, but the large radials suggest an advanced compsocrinine group such as the Carpocrinidae and comparison, with for example *Acacocrinus* Wachsmuth & Springer,1897 (see Ubaghs, 1978, fig. 272.2), show complete correspondence in all features available from the South African specimen. Ausich (1987) transferred *Acacocrinus* to the Periechocrinidae but considered it a likely ancestor of the Carpocrinidae. Identification of the South African species must await further material.

Superfamily HEXACRINITOIDEA Wachsmuth & Springer,1885
Family HEXACRINITIDAE Wachsmuth & Springer,1885
Arthroacantha Williams, 1883

TYPE SPECIES. *Arthroacantha ithacensis* Williams, 1883 from the Upper Devonian of New York; by original designation.

Arthroacantha? sp.
(Fig. 16)

MATERIAL. One set of 5 incomplete arms RO128 (part and counterpart) from Gamkapoort, Prince Albert (33°18'S, 21°38'E) in the Gydo Formation.

DESCRIPTION. Arms biserial, pinnulate, occasionally with pair of adjacent 1/2 brachials extending into strong lateral spines, occasionally with other pairs of brachials in between spinose ones bearing circular facets; pinnules long, slender, with wide groove on inner surface; adoral groove on arm moderately deep, U-shaped in section; each brachial with concave pinnular facet.

REMARKS. Identity of thes arms is very doubtful but among known spinose genera *Arthroacantha* appears to have the most similar organisation (Kesling & Chilman, 1975, pl. 135) with periodic pairs of strong spines of the same dimension and arrangement as in our specimen. However, our arms do not appear to branch at the spinose brachials which is usual in *Arthroacantha*. Nevertheless, Stewart (1940:56) noted that in a specimen from the Silica Shale at Silica, Ohio large strong tubercles are irregularly developed between the bifurcations. Goldring (1923: 290) noted a subspinose tubercle on each

1/2 brachial above the axillary secundibrach in *A. carpenteri* Hinde, 1885. There is considerable variation in the arms of *Arthroacantha* so our specimen fits within the range. However, the assignment must be extremely tentative without knowledge of the cup: an alternative is that these arms may belong to a new crinoid genus.

Subclass CLADIDA Moore & Laudon, 1943
Order DENDROCRINIDA Bather, 1899

McIntosh (1983, 1986) discussed phylogeny and classification of dicyclic cladid inadunates and concluded that the 2 suborders of Moore & Laudon (1943) and 3 suborders of Moore et al. (1978) need major review. Until that review is complete we retain all the cladids in this paper in one broad group.

Family DENDROCRINIDAE
Wachsmuth & Springer, 1886

Eckidocrinus gen. nov.

TYPE SPECIES. *Eckidocrinus interbrachiatus* sp. nov.

ETYMOLOGY. An anagram from the surname of Mr Roy Dick, who contributed much material to this study.

DIAGNOSIS. Basals hexagonal, with broad low radial ridge ornament. Radial facet >1/2 radial width, gently declivate, concave. Interprimibrach depressed, filling interradial space between primibrachs. Arms with 2 main rami per ray, with bilateral heterotomous branching; 3rd primibrach axillary; strong ramules alternating side to side along each arm from every 3rd or 4th brachial, each ramule dividing at least twice. Stem circular, large diameter, heteromorphic.

REMARKS. Among early Palaeozoic cladids bilaterally heterotomous arm branching is not widespread. Although not restricted to that family, the arm branching pattern resembles fairly closely that of the Ordovician dendrocrinid *Grenprisia* Moore, 1962 which also has brachials shaped the same as the new genus and small interprimibrachs. Family assignment is made on these tentative grounds and a specimen exhibiting the posterior of the cup will be necessary to be more definite. With available morphology it is established as a separate genus. If the similarities to *Grenprisia* are indicative of relationship it must be very distant as they are well separated in time but no other known cladid has the combination of features mentioned above.

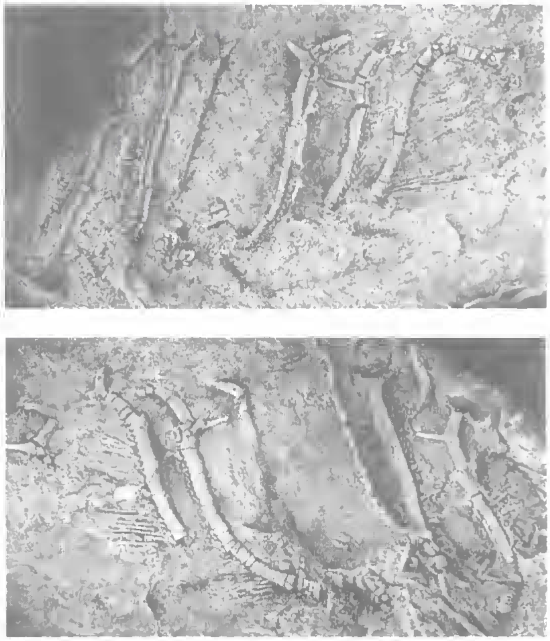


FIG. 16. *Arthroacantha*? sp., set of biserial arms with long pinnules and paired spines, RO 128a and b, ×1.5.

Eckidocrinus interbrachiatus sp. nov.
(Fig. 17)

MATERIAL. HOLOTYPE: B4534. PARATYPE: B4554 from the Voorstehoek Formation, at Matroosberg, Stinkfontein, Hex River Pass.

DIAGNOSIS. As for genus.

DESCRIPTION. Cup broadly conical (holotype 16mm max. diameter), short (holotype 9mm long); plates smooth, with broad low radial ridges and depressed corners in most parts of cup. Infrabasals 5, visible laterally, pentagonal, short, wider than long. Basals 5, largest plate in cup, hexagonal, with broad low ridges from infrabasals to radials and similar transverse ridge to adjoining basals, distal tip of basals depressed as are lateral parts, ridges less obvious at infrabasal to basal sutures. Radials 5, pentagonal, with scallop of radial facet in upper margin, with ridges running from basals towards facet and another similar ridge running laterally around cup near distal edge of radial circlet; radial facet >1/2 width of radials, a little less than semicircular, declivate, concave. Primibrachs 3, 2 subquadrate, wider than long; 3rd primibrach axillary, pentagonal. Interprimibrachs filling interradial notch to approximately base of 3rd

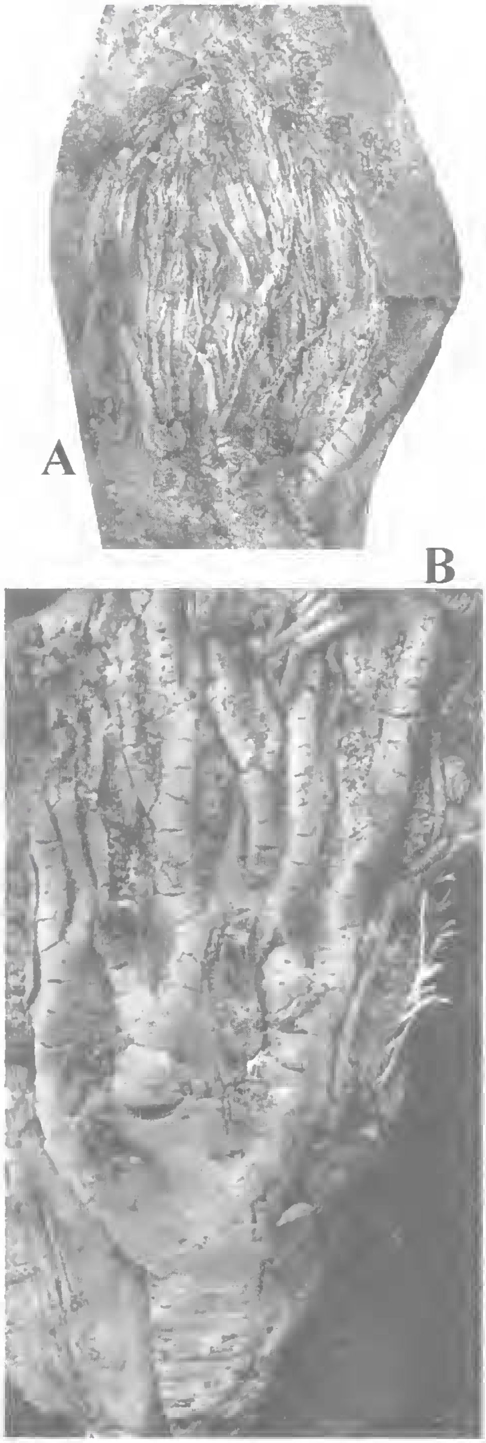


FIG. 17. *Eckidocrinus interbrachiatus* gen. et sp. nov. A, set of arms viewed from inside, B4554, ×1. B, holotype crown showing uniserial repeatedly branching arms, B4534, ×2.

primibrach plate, 3 larger plates resting on radials, becoming smaller distally. Arms bilaterally heterotomous, with 2 main arms per ray, with strong ramules (at least 6 per ramus) alternating from side to side along each arm at about every 3rd or 4th brachial, with ramuli dividing at least twice; full extent of arms not clear; ventral groove deep, broadly V-shaped in section, with large cover plate series, about 3 or 4 per brachial. Anal area of cup not available; anal sac longer than arms, straight, of small strongly ornamented plates, apparently perforated. Stem circular, heteromorphic, with noditaxis N3231323.

REMARKS. Part of the anal sac is preserved at the right of the arms in one specimen (Fig. 17A). The anal sac appears to have been long and composed of a few columns unornamented plates.

Family CYATHOCRINITIDAE Bassler, 1938
Kopficrinus Goldring, 1954

TYPE SPECIES. *Kopficrinus pustuliferus* Goldring, 1954 from the Lower Devonian of New York; by original designation.

REMARKS. Goldring's genus, for which the anal structure has been unknown except for the anal X supporting 3 small anals, was assigned to the Gasterocomidae by Moore et al. (1978) which family lacks an anal tube and has the anal opening through the side of the cup below the posterior radials. Thus the anal opening somewhere above the cup in the type species does not fit the family concept. The second species of the genus, described herein, with a long anal tube also argues against assignment to Gasterocomidae. We assign the genus to the Cyathocrinitidae based on the symmetrical anal plating, anal tube, the small pentagonal infrabasal circlet and the enlarged posterior basal.

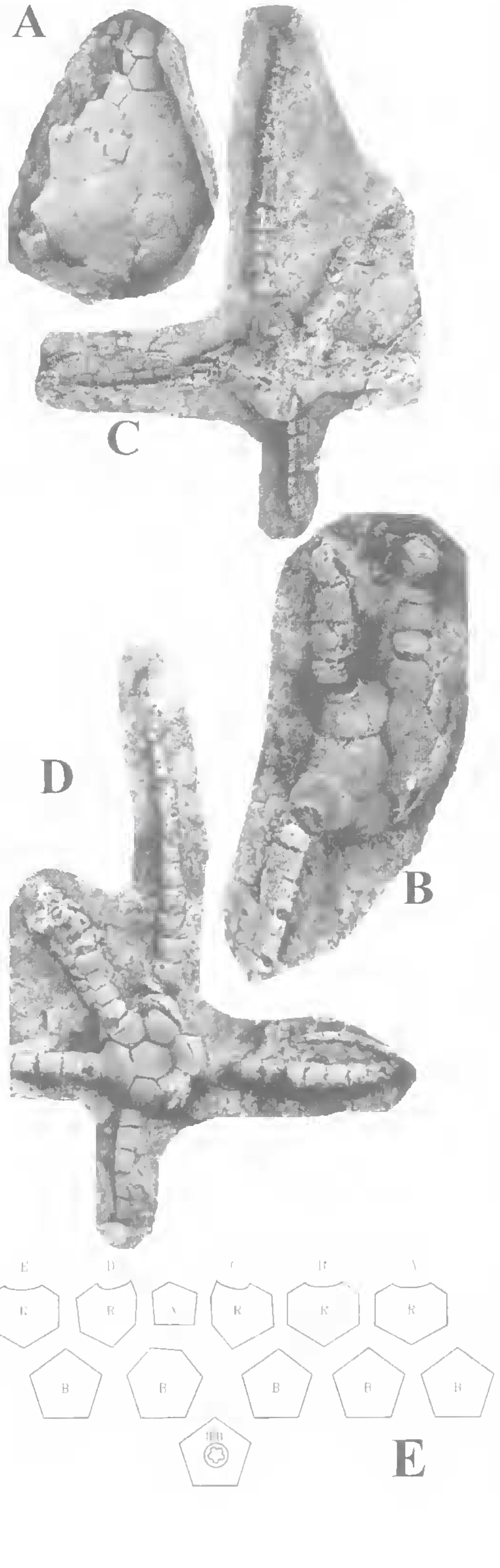
Kopficrinus halbichi sp. nov.
(Fig. 18)

Ophiurites sp. Rossouw, 1933: 75, fig.2.

ETYMOLOGY. For Prof. I.W. Halbich, Stellenbosch University, who kindly made this material available.

MATERIAL. HOLOTYPE: SUK466. PARATYPE: SUK464 (2 specimens on one piece of rock (1 drawn by Rossouw, 1933), from the first shale band on Vredenhof, Prince Albert (locality quoted by Rossouw (1933) in the Gydo Formation.

DIAGNOSIS. Infrabasal circlet apparently fused; arms atomous (or with at least 14



primibrachs); anal sac of 4 columns of hexagonal sutured plates.

DESCRIPTION. Cup low, bowl-shaped, smooth. Infrabasal circlet pentagonal, apparently fused into a single plate, most of circlet visible in side view. Basals 5, pentagonal except for hexagonal posterior basal. Radials 5, with narrow angustary and declivate horseshoe-shaped facets, without axial canal separate from ventral groove. Anal X in radial circlet, slightly proximal to adjacent radials, resting symmetrically on posterior basal, with horizontal distal margin supporting 3 small anal plates at base of tall anal tube. Anal tube of 4 columns of close-packed hexagonal plates (distal end and anal opening not clear). Arms atomous (longest section available 14 brachials long). Stem circular in section, with vaguely pentalobate lumen.

REMARKS. Rossouw (1933, fig.2) gave a line drawing only of the specimen he identified as an ophiuroid and which is here designated a paratype of this new crinoid species. The line drawing was inaccurate in several details which are corrected here with a photograph (Fig. 18C,D), for example the specimen shows 3 of the 4 columns of plates in the anal tube whereas Rossouw's figure shows only 2. The latex cast from the counterpart of Rossouw's specimen gives the oral aspect, with the mouth area unclear: oral plates are not clear but may be assumed to have been present from the edges of the radials.

This species is assigned to *Kopficrinus* based on the matching posterior plating of the cup, the radial facets, the large round brachials and in particular the apparently atomous arms. Distal tip of any arm is not available in either the type or the new species but in both, arm sections are known with 13 or 14 brachials. Thus it is uncertain if the arms are atomous or not but it seems unlikely, from comparison with other crinoids, that these arms would divide for the first time so far from the cup: we consider the arms were most likely atomous.

FIG. 18. *Kopficrinus halbichi* sp. nov. A, cup showing infrabasal circlet and anal tube (12 o'clock), SUG464, ×4. B, cup SUG464-1, ×4. C-D, oral and basal views of holotype cup SUG466a and b, ×3.5. E, sketch of plate arrangement with infrabasals shown as circlet with size of stem facet and section of central canal indicated. IB = infrabasal; B = basal; R = radial; X = anal X; A-E above radials indicate rays.

Family EUSPIROCRINIDAE Bather, 1890
Monaldicrinus gen. nov.

TYPE SPECIES. *Monaldicrinus johni* sp. nov.

ETYMOLOGY. An anagram for John Almond, Geological Survey of South Africa, Capetown, who greatly assisted us during this project.

DIAGNOSIS. Cup low, strongly flared laterally. Infrabasals 5. Basals 5. Posterior basal heptagonal, supporting 2 almost equally sized anal plates distally. C radial virtually symmetrical distal to BC basal. Anal sac large and long, with opening at tip, with main column of plates both externally and adaxially. Arms 10, uniserial, stout, dividing isotomously once, ramulate; ramules alternating from side to side on every 5th brachial, dividing isotomously on 6th tertibrach. Stem circular in section, small diameter for the family, with moderately large lumen vaguely pentalobate in section.

REMARKS. This genus is assigned to the Euspirocrinidae on the arrangement of anal plates in the cup which arrangement compares closely with *Parisocrinus* Wachsmuth & Springer, 1880 and *Ampheristocrinus* Hall, 1879, on the nonpinnulate arms, on the 5 infrabasals and basals, on the ambulacral groove cover plates and on the circular stem. It is distinctive in its arms branching only once isotomously, in being ramulate and their arrangement, in the nature of the large anal sac, in the low flared shape of the cup which does approach *Vasocrinus* Lyon, 1857 and in the relative diameter of arm to stem. The anal plate arrangement is also found in *Poteriocrinites* (see Moore *et al.*, 1978, fig.394.7) but that genus of the Poteriocrinina has pinnulate arms which is used by Moore *et al.* (1978) as a subordinal discriminator. The arm structure of *Monaldicrinus* occurs in the Barycrinidae but that family has a distinctly different anal plate arrangement. However, in discussing the Barycrinidae, Moore & Laudon (1943:40) considered the single isotomous branching followed by development of alternating ramules (their branchlets) to be a primitive stage of development leading to pinnulation. They also considered the transverse ridge on the articular facet, seen in *Monaldicrinus*, an advanced feature. It is tempting to suggest that perhaps *Monaldicrinus* from the Malvinokaffric Province was an advanced cyathocrininid ancestral to the Poteriocrinina.

Monaldicrinus johni sp. nov.
(Figs 19-21)

MATERIAL. HOLOTYPE: SAMK977, an external mould from 100m N of the house at Wolfaardt's Farm, Riet Valley, near Ceres. PARATYPES: B4579 from Hex River Pass, 1.3 miles from Great Swaarmoed Farm; SAM3947 from Laken Vlei, Ceres (1st Shale); RO202 and 810 from Gamkapoort, Prince Albert, 33°18'S, 21°38'E (C2S1).

DIAGNOSIS. As for genus.

DESCRIPTION. Cup smooth, small relative to size of crown, 15mm long, conical. Arms apparently elevated only 10-20° above horizontal. Infrabasals 5, pentagonal, uniform in size, almost completely visible and as long as wide in side view. Basals 5, hexagonal except for heptagonal BC and CD basals, base against infrabasals with obtuse angle (>150°) at central junction with suture between infrabasals. Radials 5, large, wider than long, heptagonal; radial facet only slightly declined outwards, peneplenary. Facet on 1st primibrach with strong transverse ridge broken by central gap, with large circular canal just beneath broadly V-shaped ambulacral canal. Circular canal migrating through the gap in transverse ridge by 5th primibrach to be close to outer edge of facet and well removed from sharply V-shaped ambulacral groove. Ambulacral groove covered by thick cover plates; cover plates more numerous than brachials (c. 8 to 5) but exact correspondence unclear. CD basal supporting hexagonal anal X and pentagonal radianal; radianal resting symmetrically on BC and CD basals, supporting the right tube plate (3rd anal plate in cup) adjacent to the C ray. Anal sac large, with terminal aperture, with numerous (>10) vertical columns of polygonal plates; some columns with plates having scalloped lateral margins (scallops never on proximal or distal margins) with perforations through wall at each scallop; perforations most prominent near base disappearing before tip; main column of larger plates on outer side distal to anal X and on inner side rising from oral area; main column on inner side with short stubby spine usually on every 2nd plate but irregular and sometimes on consecutive plates; such spines less frequent and more irregular on some other columns on inner side but not on outer side of sac. Arms 10, each ray with 1 isotomous branching at axillary primibrach 8 (B4579)-12(RO810). Above this 1 specimen (RO202) with ramules developed alternately on each 5th secundibrach; 1st ramule on outside of ray; ramule branching isotomously at least twice

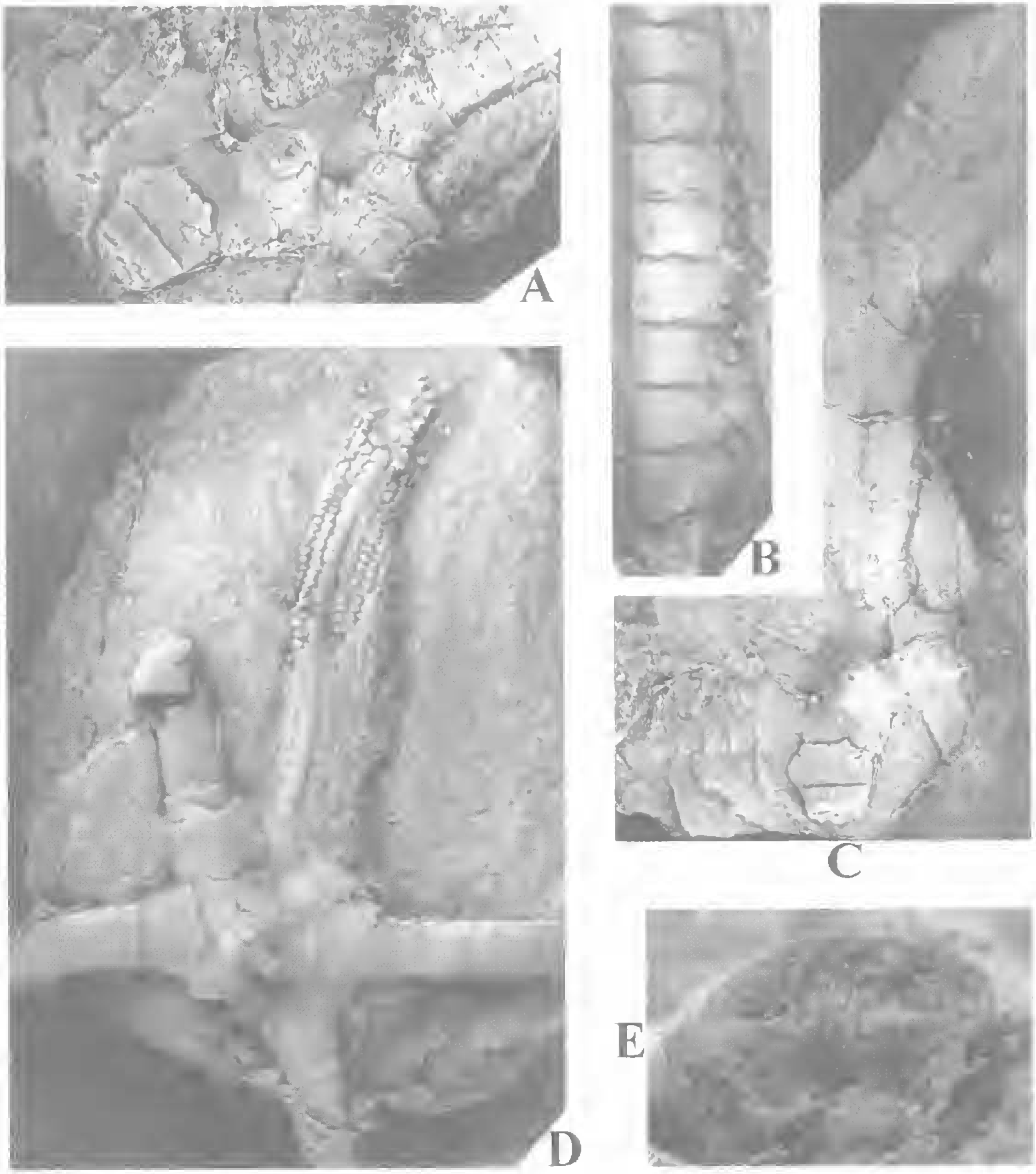


FIG. 19. *Monaldicrinus johni* gen. et sp. nov. A,C,E, RO 810. A, cup ×2. C, cup showing stout uniserial arm, ×1.2. E, distal face of first primibrach ×6. B, part of an arm showing ambulacral cover plates B4549. ×6. D, holotype SAM K977, ×2.

each time at 5th brachial, circular in section, shorter than 4 secundibrachs, standing up vertically off the arm. Stem circular in section, small diameter for the family and relative to cup, with moderately large lumen vaguely pentalobate in section.

REMARKS. The 4 specimens of the cup have the arms splayed out horizontally or almost so, mostly in the bedding plane. Also in each is a

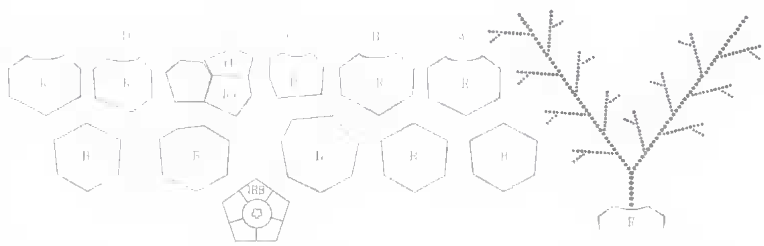


FIG. 20. *Monaldicrinus johni* gen. et sp. nov. sketch of plate arrangement (infrabasals shown as circlet with size of stem facet and section of central canal indicated) and arm branching (on right). IBB = infrabasal circlet; B = basal; R = radial; RA = radianal; X = anal X; rt = right tube plate; A-E above radials indicate rays.

degree of dislocation and dislodgement along sutures and fracture across plates within the cup. These taphonomic features make it difficult to interpret original cup shape and arm attitude. In so far as the plates are in contact around the cup at the radial circlet we could interpret minor flattening of the cup. However, in Fig. 19D where the anal sac is assumed to have been vertical in life but is now horizontal, the dislocation of plates near its base is minimal and certainly does not suggest such a change in attitude after death. We therefore, have no reason to believe the horizontal arm position reflects the original attitude. While it is more likely, by comparison with other cladids, that the arms were erect, the much smaller stem diameter, relative to crown size in *Monaldicrinus* which is a fairly large crown among crinoids in general may suggest either 1, it lived in quiet water and so did not need strong attachment in currents (unlikely given the enclosing clastic sediments but nevertheless the animal is found in the finer shale layers and may have migrated with the environment) or 2, that the arms were less erect and thus less of a baffle to currents. What ever the answer, we consider that the arms were probably not completely erect but that the ramules coming off them were probably vertical. In the 3 specimens with 4 rays preserved the A ray is missing and the plating near its base is unclear. In Fig. 19D there is the suggestion that it may lie on the basals but with only point contact to the other radials rather than a sutured junction of some length. We cannot be certain of this point due to preservation but if so this would provide a strong accentuation of the A ray - CD interray line of symmetry.

The large specimen of the oral side of the arms and anal sac (Fig. 21C) is assigned to this species on the nature of the anal sac, size and nature of the arms and their branching pattern. Although very difficult to see on the latexes, ramules are identified on the mould of Fig. 21B (because of the penetration of limonite) at every 5th secundibrach. The prominent tubercles on that specimen which are lacking on other specimens are interpreted as only occurring on the oral side of the anal sac and thus not evident on the other specimens of the outer side. Without moulds of the 2 sides from the 1 individual this cannot be confirmed. Until it is determined objectively we remain confident of our identification.

Family THALAMOCRINIDAE Miller & Gurley, 1895

Following McIntosh & Brett (1988) this family name replaces Bactrocrinitidae Jaekel, 1918 as used by McIntosh (1979; 1983). *Sacrinus* is assigned to this family based on its affinity to *Follicrinus* which was assigned to the Bactrocrinitidae by McIntosh (1979, 1983) and although excluded by McIntosh & Brett (1988) is retained in the family herein. Family level subdivision of the cladids remains in flux so we adopt a broad family concept here. We acknowledge that quadrangular vs. pentagonal radianal plate could indicate entirely separate lineages but this has not been demonstrated and is not applied herein.

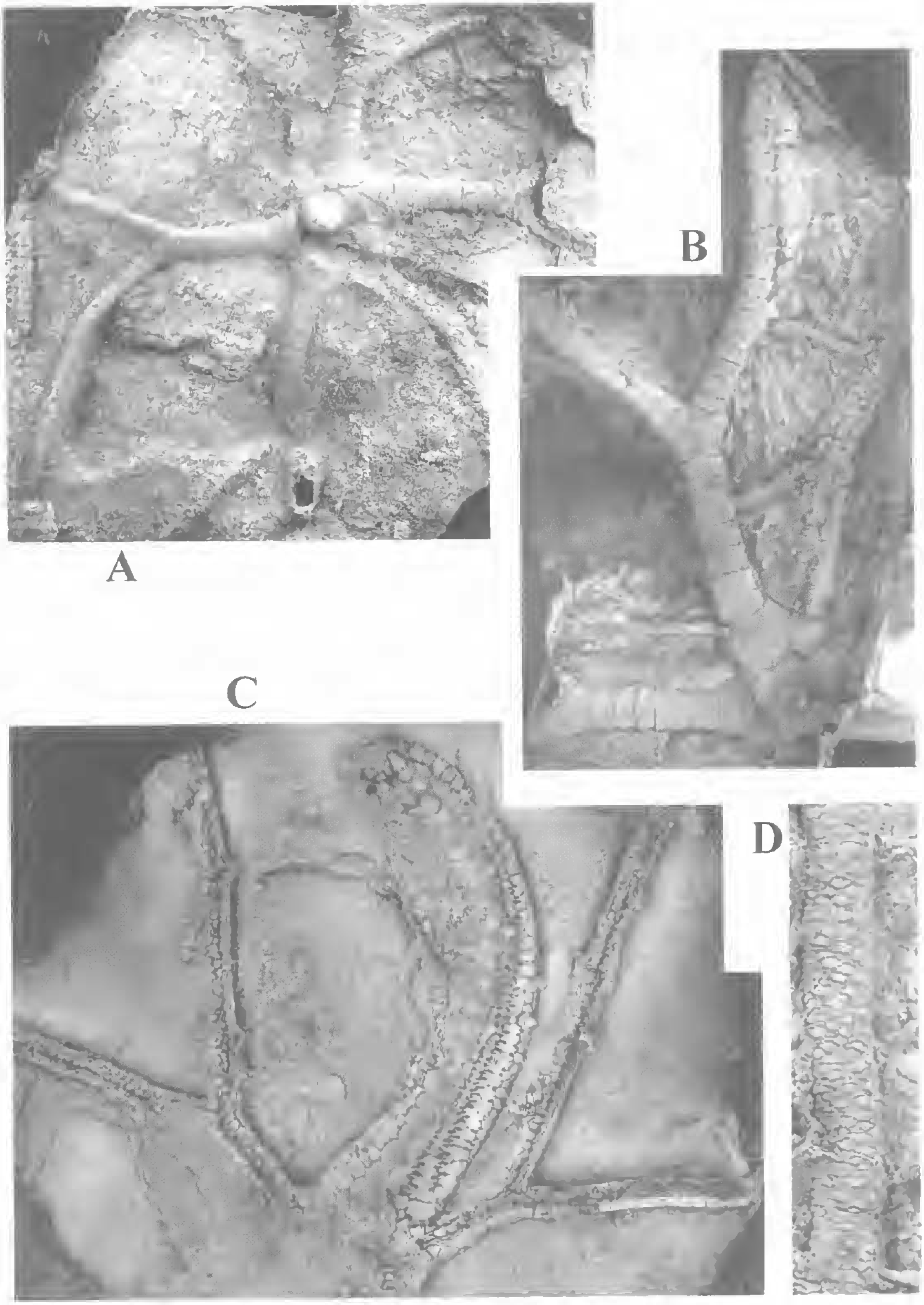
Sacrinus gen. nov.

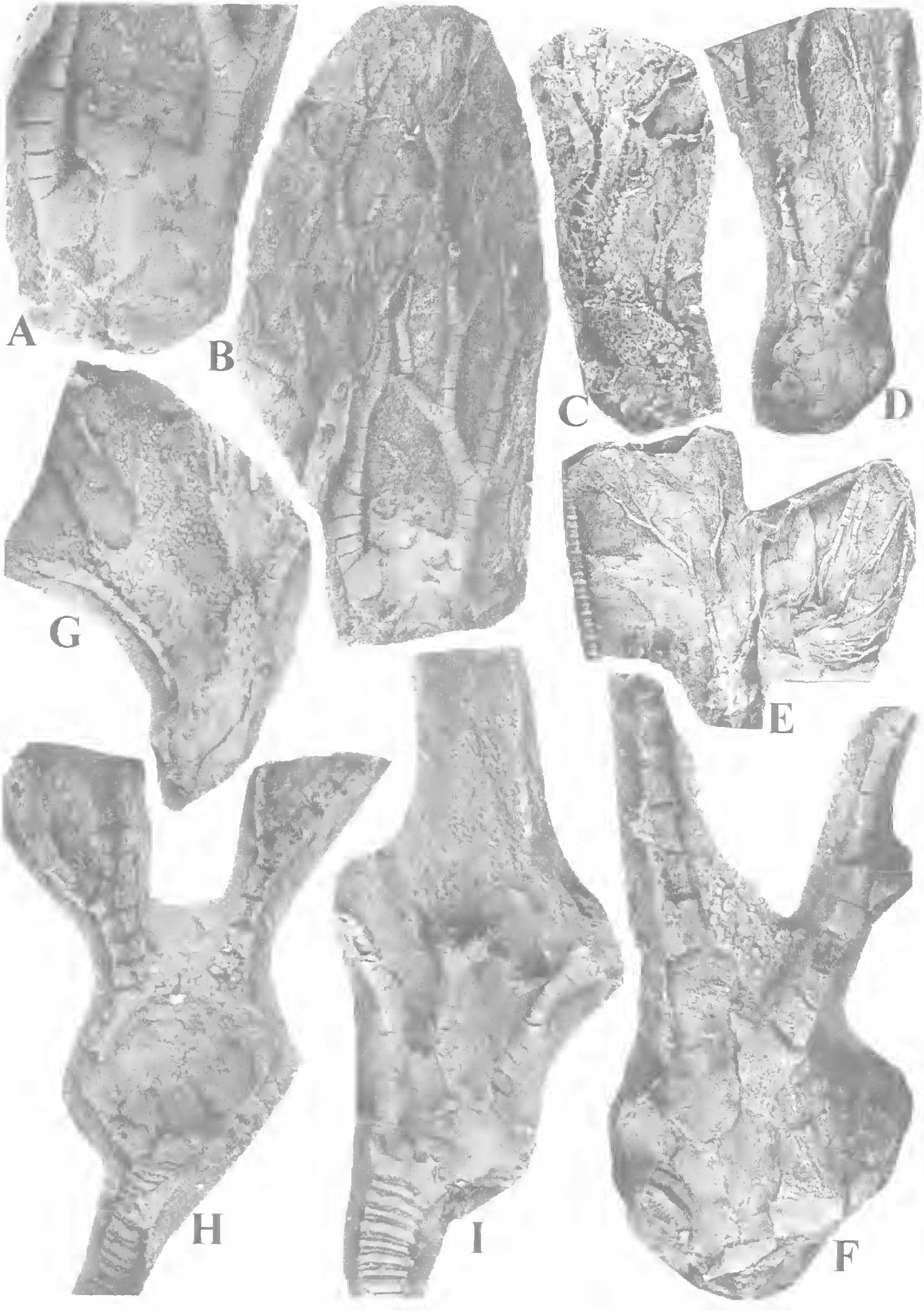
TYPE SPECIES. *Sacrinus gamkaensis* sp. nov.

ETYMOLOGY. Sa- for South Africa.

DIAGNOSIS. Cup conical; infrabasals approximately same length (or only slightly shorter) as basals; radials wider than long, with angustary radial facets projecting laterally. Anal plates in cup 3, with broad low radial ridge

FIG. 21. A-C, *Monaldicrinus johni* gen. et sp. nov. A, crown splayed on bedding plane in proximal view, SAM3947, ×1. B, crown showing anal tube on right B4579, ×2. C, set of arms showing cover plates and widely spaced ramules and large anal tube RO 202, ×1. D, stem indet., section of distinctive indeterminate stem in lateral view RO 295a, ×4.


A
B
C
D


A
B
C
D
G
E
H
I
F

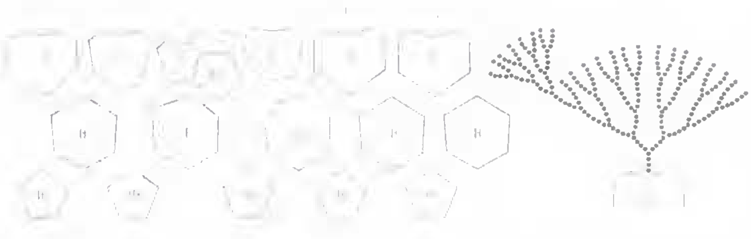


FIG. 23. *Sacrinus gamkaensis* gen. et sp. nov., sketch of plate arrangement and arm branching (on right) with distal branching shown on only one branch but symmetrical on each other branch. IB = infrabasal; B = basal; R = radial; RA = radianal; X = anal X; rt = right tube plate; A-E above radials indicate rays.

ornament; radianal pentagonal, proximal and left of C radial, directly supporting right tube plate; anal X not much larger than radianal; anal tube large, inflated, irregularly shaped, of many very small polygonal plates irregularly arranged. Arms robust, branching isotomously 3 or 4 times. Stem pentagonal to subrounded in section, heteromorphic.

REMARKS. The major distinguishing feature of this new genus and of *Follicrinus* Schmidt, 1934 (type *Taxocrinus*? *grebei* Follmann, 1887) from the Lower Devonian of Germany is the irregularly shaped, inflated anal sac of small irregularly arranged stellate plates. McIntosh (1983) queried whether this feature alone should carry generic status, particularly in the absence of knowledge of the anal sac in *Bactrocrinites fusiformis* Roemer, 1844, the type of *Bactrocrinites*. In *Follicrinus* the radianal is quadrate, there are only 2 anal plates in the cup, the radial facets may be interpreted as plenary (as by Moore et al. (1978) who clearly thought so by placing it in the Mastigocrinidae) and the stem is circular in section and composed of long columnals. In *Sacrinus* the radianal is pentagonal, there are 3 anal plates in the cup, radial facets are clearly peneplenary and protruding and the stem is heteromorphic and pentagonal in section. Despite these differences cup shape including shape and proportions of most individual plates, robustness and branching of the arms, size and plate ornament and arrangement of the anal sac and tuberculate ambulacral cover plates indicate a fairly close relationship between the 2 genera. We note some comparison with Ordovician *Grenprisia* Moore, 1962 in the very large cylindrical to inflated anal sac of small stellate or smooth plates, the 5- or 6-sided radianal, short wide radials and pentagonal stem. However, these comparisons could very well reflect parallel evolution and without intermediate forms no suggestion of affinity is made. The distinctive anal structure makes comparison with other cladids rather unnecessary.

Sacrinus gamkaensis sp. nov.
(Figs 22-25)

ETYMOLOGY. From Gamkapoort.

MATERIAL. HOLOTYPE: ROC25. PARATYPES: RO127, 255, 731, L7, C25, B4522, B4523, B4526, B4527 and B4530 all from Gamkapoort, all from the Gydo Formation. OTHER MATERIAL: B4574 from the Hex River Pass area on Montagu Road, 14km from the N9 turnoff; RO283 from Swaarmoed Pass, Ceres, 33°21'30"S, 19°30'30E; and ROT15 from Matroosberg, Worcester (Hex River Pass), 33°30'S, 19°49'E; all in the Voorstehoek Formation. B4669 from the quarry on E of road N from Prince Alfred's Hamlet, about 1km S of Gydo in the Gydo Formation.

DIAGNOSIS. Radials and basals with broad low ray ridges. Anal plates in cup 3; anal X only just larger than pentagonal radianal; anal plates and proximal anal sac plates with distinct ray ridges; anal sac long, cylindrical to moderately inflated, composed of many tiny stellate polygonal abutting plates. Arms isotomous, 1st branching on 4th, 5th, or 6th primibrach. Stem subpentagonal in section, heteromorphic.

DESCRIPTION. Cup conical, up to 5mm long, with broad low radial ridges and (in some specimens) ornament of fine lines on top of ridges. Infrabasals 5, pentagonal, slightly wider than long (max). Basals 5, hexagonal except for heptagonal BC basal, with radial ridges forming a broad cross. Radials wider than long; articulating facet angustary, about 0.5 of plate width, only slightly declined, almost circular, projecting

FIG. 22 *Sacrinus gamkaensis* gen. et sp. nov. A-B, crown in C-D interray view showing base of anal tube and arm branching RO 255, ×6 and ×4, respectively. C, anal tube and interior of some arms RO L7a, ×2. D-F, crown showing arm branching and ornament on cup RO C25, ×2, ×1 and ×3, respectively. G, crown showing anal tube, RO T21, ×3. H, interior view of crown RO 127, ×4. I, crown viewed from side opposite anal interray showing anal tube RO T18, ×3.

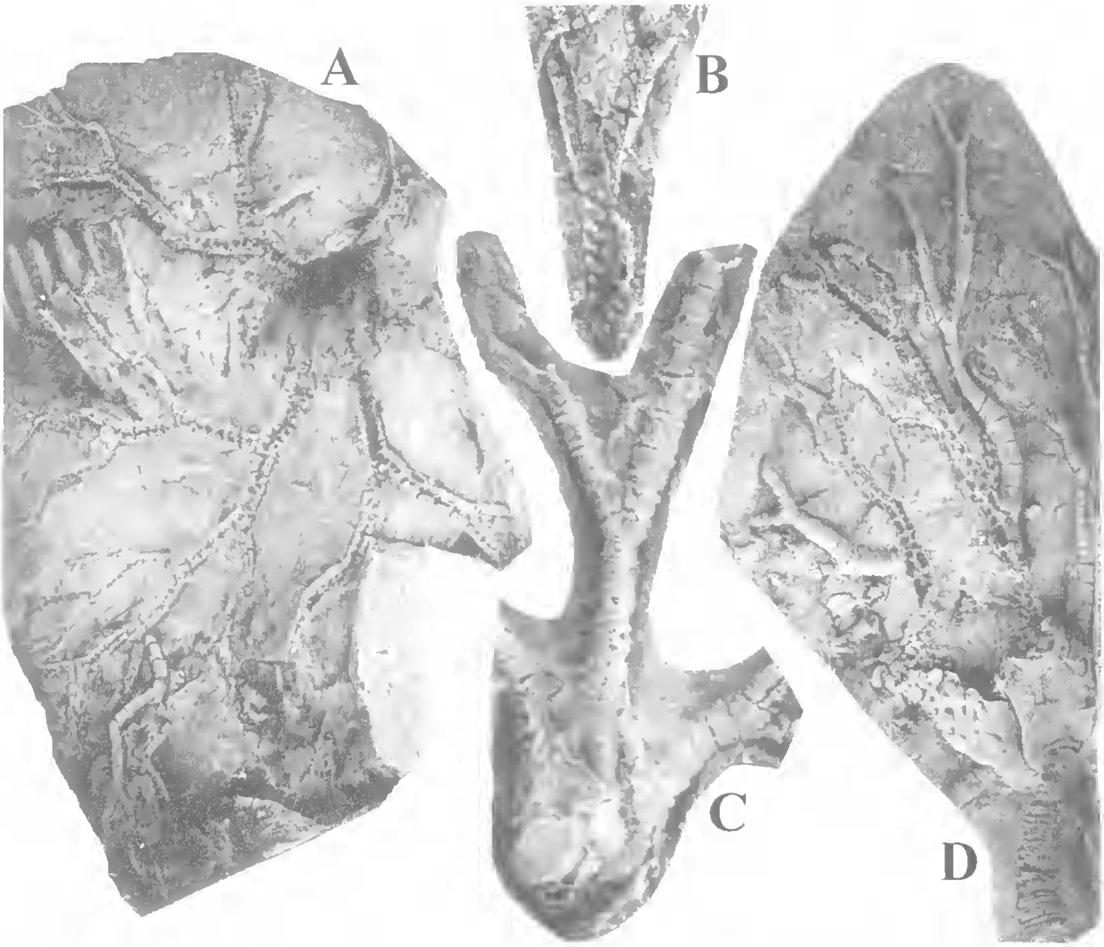


FIG. 24. *Sacrinus gamkaensis* gen. et sp. nov. A, crown in ambulacral view of arms and internal mould of cup RO 731, ×2. B, ambulacral view of arm showing small cover plates RO 255, ×5. C, partial crown showing ray ridges on radials RO T25, ×3. D, crown showing ornament on anal tube RO L7, ×3.

laterally; radial ridges radiating from arm base in 4 directions towards centre of 4 lower sides (i.e. 2 cross to adjoining basals and other 2 laterally onto adjoining radials or radianal in case of C radial). Anal plates in cup 3, with radiating ridges directed to the middle of each side, with all 3 way sutural junctions depressed; anal X hexagonal, directly distal to CD basal, contacting D radial and other 2 anal plates towards C ray; radianal pentagonal, proximal and left of C radial, contacting BC and CD basals; right tube plate directly distal to radianal. Anal sac subcylindrical, inflated irregularly, reaching distally to about 3rd arm division, of many tiny irregularly polygonal abutting plates, aperture not observed; each plate with radial ridge ornament continuing and becoming finer distally. Arms slender, branching isotomously 7 times, laterally compressed in cross section, with deep adoral groove, with column of tiny cover plates on either side of groove; primibrachs 4, 5 or 6 axillary; in 2nd and more distal brachial series 5th brachial usually axillary (variable between or within arms even in 1 specimen). Stem subcircular to subpentagonal in section, noditaxis N3231323, with latus projecting laterally on nodals.

REMARKS. *Sacrinus gamkaensis* is distinguished from *S. hexensis* by the radial ornament on its anal cup plates and anal sac, the latter being smooth. A few specimens of the type species also show a very fine multiple ridge ornament (Fig. 22D, F) on top of the broad radial ridge ornament that is the specific distinguisher. Some specimens

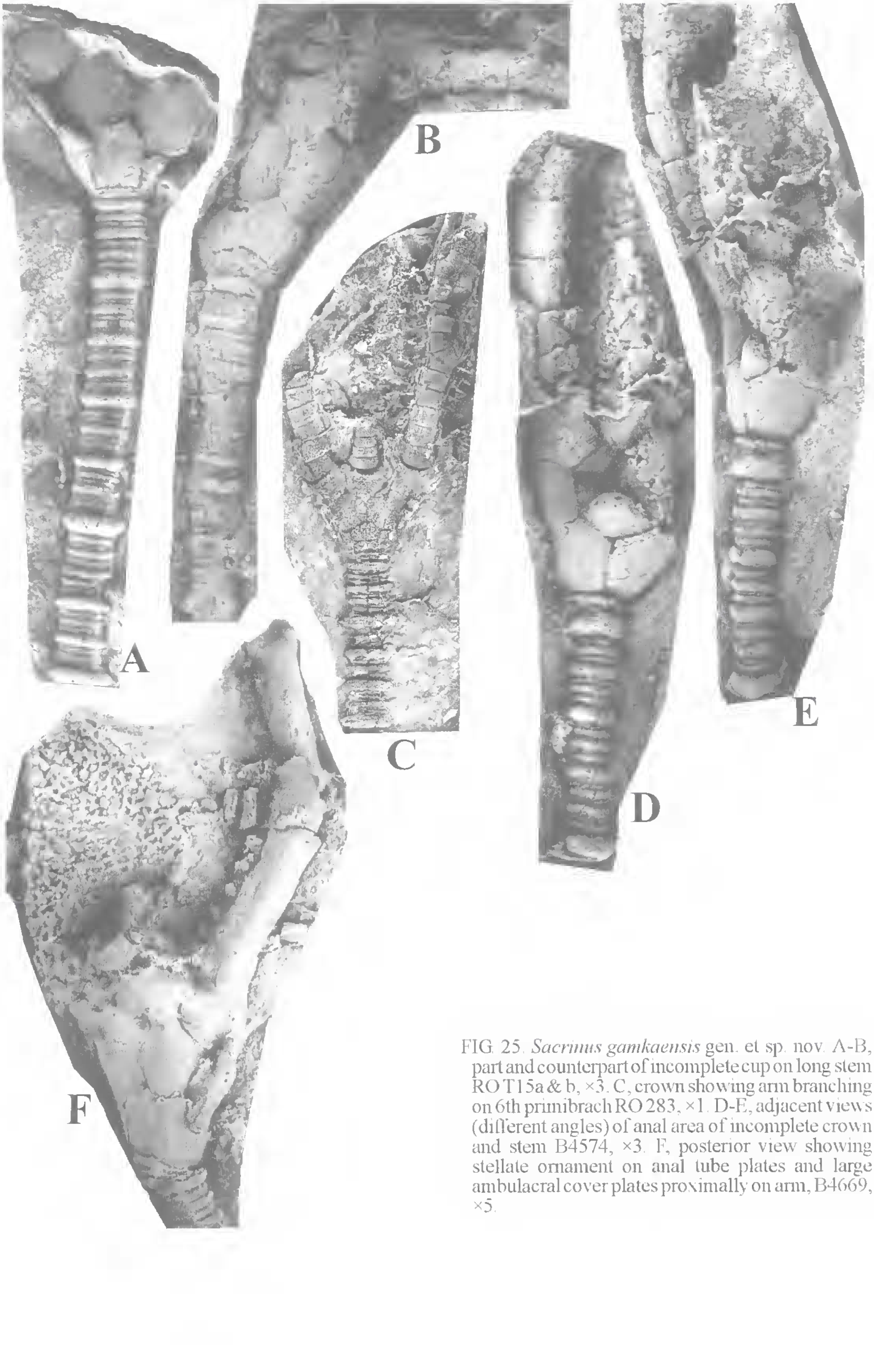
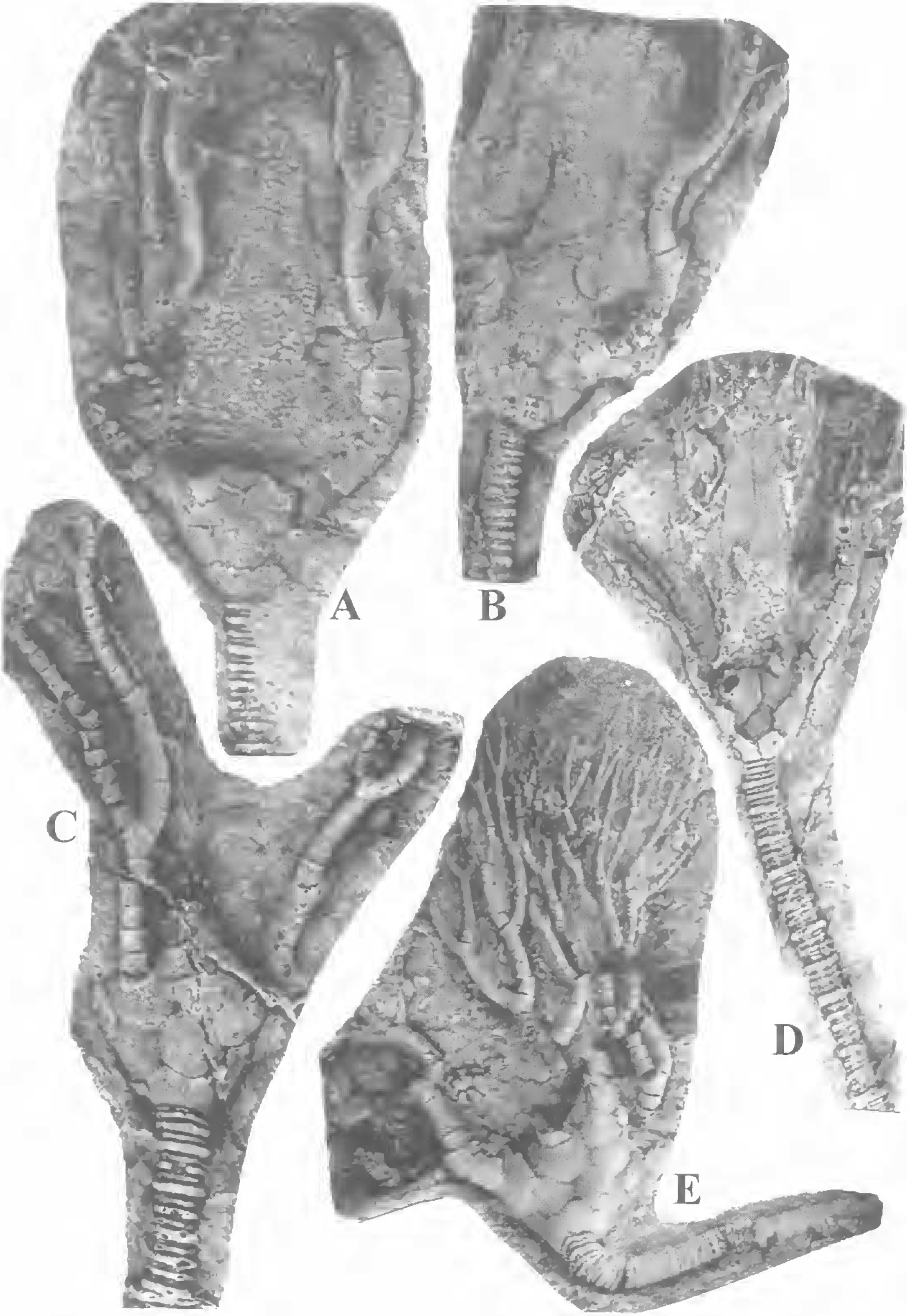


FIG. 25. *Sacrinus gamkaensis* gen. et sp. nov. A-B, part and counterpart of incomplete cup on long stem RO T15a & b, ×3. C, crown showing arm branching on 6th primibrach RO 283, ×1. D-E, adjacent views (different angles) of anal area of incomplete crown and stem B4574, ×3. F, posterior view showing stellate ornament on anal tube plates and large ambulacral cover plates proximally on arm, B4669, ×5.


A
B
C
D
E

(Figs 22A, 25C) suggest a pustulose surface on radial plates and in others (Fig. 24C) the radial ridge ornament is well developed on radials as well as anal cup plates. Variation noted here is considered intraspecific.

Sacrinus hexensis sp. nov.
(Fig. 26)

ETYMOLOGY. From the Hex River Pass.

MATERIAL. HOLOTYPE: B4571a (lower specimen of 2 close together). PARATYPES: B4571b (other 2 specimens), B4572, PRV HR5 all from Hex River Pass on Montagu Road, 14km from N9 turnoff (C2S2).

DIAGNOSIS. Cup plates including anal plates and anal sac plates smooth; anal sac long, subcylindrical, of many small polygonal abutting plates; 1st arm branching variable at 3rd-6th primibrach.

DESCRIPTION. Cup short, conical, with smooth plates, up to 5mm long. Infrabasals 5, pentagonal, as long as wide (max). Basals 5, hexagonal except for heptagonal CD basal. Radials wider than long in lateral view, with 6 sides plus radial facet; radial facet angustary, about 0.5 of plate width, only slightly declined, almost circular. Anal plates in cup 3; anal X hexagonal, distal to CD basal, contacting D radial and other 2 anal plates towards C ray; radianal pentagonal, proximal and left of C radial, contacting BC and CD basals; right anal tube plate distal to radianal. Anal sac subcylindrical, reaching distally to about 3rd arm division, composed of many tiny smooth polygonal abutting plates, opening terminal, with circlet of elongate plates around aperture. Arms slender, branching isotomously 4 times, laterally compressed in cross section, with deep adoral groove, with columns of tiny cover plates on either side of groove; primibrachs 3, 5, 6 or 7 axillary; similar variation in subsequent brachial series, number of brachials between axillaries not consistent even within one specimen. Stem subpentagonal to subrounded, heteromorphic, noditaxis N3231323; nodals slightly longer and wider, with rounded latus.

REMARKS. This species is distinguished from *K. gamkaensis* above.

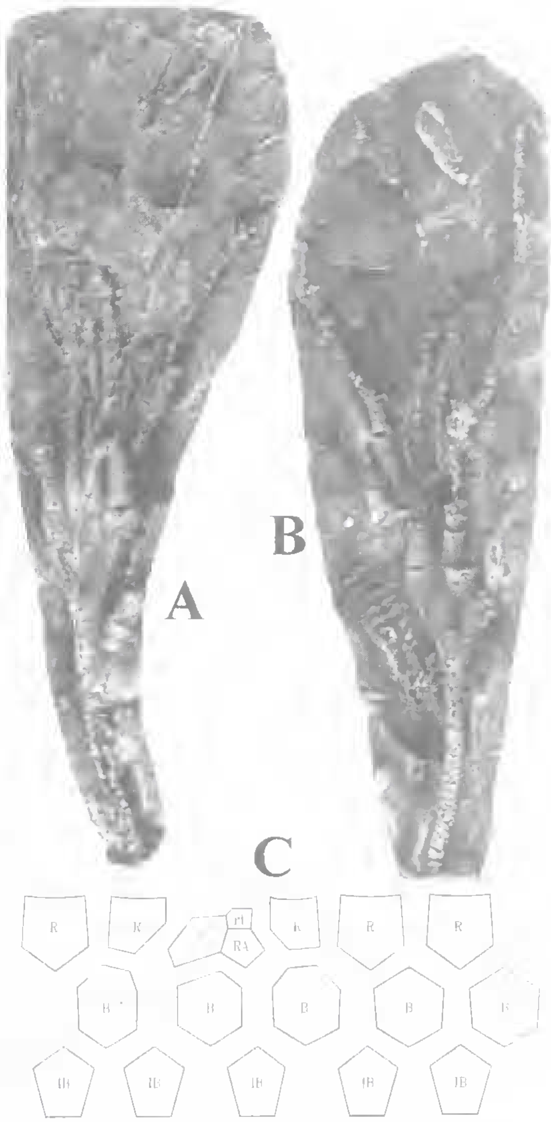


FIG. 27. *Cradeocrinus plenarius* sp. nov. A-B, holotype crown B207A, ×5. C, sketch of plate arrangement. IB = infrabasal; B = basal; R = radial; RA = radianal; X = anal X; rt = right tube plate.

Cradeocrinus Goldring, 1923

TYPE SPECIES. *Cradeocrinus elongatus* Goldring, 1923 from the Upper Devonian West Falls Group of western New York; by original designation.

FIG. 26. *Sacrinus hexensis* gen. et sp. nov. A, crown showing anal tube from side of cup opposite C-D interray B4571c, ×5. B- C, holotype crown in A ray and C-D interray views B4571a & b, ×4, respectively. D, crown in A-E interray view B4571D, ×3. E, crown with D radial central and anal cup plates to right HR-5, ×5.

Cradeocrinus plenarius sp. nov.
(Fig. 27)

ETYMOLOGY. For the plenary radial facets.

MATERIAL. HOLOTYPE: B0207 from the Waboomberg Formation at Boplaas Farm, N of Ceres.

DIAGNOSIS. Cup long, cylindrical, very small; plates smooth. Radial facets plenary. Three anal plates in cup; radianal pentagonal, contacting 1st right tube plate; anal sac long slender, of 8-10 columns of polygonal plates, perforated in sutures. Arms slender, of long brachials with shallow ventral groove, branching isotomously at 4th primibrach.

DESCRIPTION. Cup small, 2.2mm long, 1.2mm max diameter, high conical; plates smooth. Infrabasals 5, equal, long, pentagonal in lateral view. Basals 5, hexagonal, longest plates in cup. Radials 5, pentagonal, with plenary radial facets. CD interray wide, with 3 anal plates in cup, and proximal 1/2 of 2 others just in cup, anal X and radianal each supporting column of plates rising into anal sac; radianal pentagonal, proximal and left of C radial, contacting right tube plate; anal sac at least 10mm long, of 8-10 columns of regular hexagonal plates, with depressions leading to perforations in the sutures. Arms very slender, tapering strongly over 1st 2 primibrachs, long (longest available incomplete at 19mm), with 4th primibrach axillary, branching at least twice distally but type of subsequent branching uncertain (probably heterotomous with ramules from shapes of axillaries available), non-pinnulate; primibrachs more than twice as long as wide, with shallow ventral groove. Stem circular in section, heteromorphic, with alternating long and short columnals of uniform diameter, tapering for proximal 10mm then uniform in diameter, full length unknown.

REMARKS. This species is distinguished in the genus by its plenary radial facets (other species have peneplenary facets), small size, smooth plates, and very slender arms. It has the cup shape of *C. elongatus* and the anal sac structure of *C. nanus* (Roemer,1863) (Schmidt,1934, fig.24) but in combination its features are separate.

Thalamocrinus Miller & Gurley, 1895

TYPE SPECIES. *Thalamocrinus ovatus* Miller & Gurley, 1895 from the Ludlovian Brownsport Formation in Tennessee; by origianal designation.

REMARKS. McIntosh & Brett (1988) reviewed the genus in detail providing a clear basis for comparison. The South African material is not as well preserved as most of the North American species and on only one South African specimen is the posterior interray available, and then not clearly. However, the radianal, although pentagonal is similarly placed and the anal X is in the radial circlet, the cup is barrel-shaped to only very slightly flaring, the plates are of similar thickness and the proximal part of the stem is very similar with nodals much larger than internodals and well rounded laterally. *T. arenaceus* is distinguished within the genus by its very short infrabasal circlet.

Thalamocrinus arenaceus sp. nov.
(Fig. 28)

ETYMOLOGY. For the sandstone matrix of all specimens.

MATERIAL. B4538 and B4556 (numerous cups and arm and stem fragments on each slab) from the Gamka Formation at Grootrivier Hoogte.

DIAGNOSIS. Infrabasals short in lateral view.

DESCRIPTION. Cup barrel-shaped to slightly flaring at radials, about as long as wide (6-8mm in available specimens); plates smooth, convex, thick. Infrabasals 5, very short and pentagonal in lateral view. Basals 5, hexagonal, as wide as long; posterior basal heptagonal. Radials 5, pentagonal; radial facet angustary. Three anal plates in cup; radianal pentagonal, proximal and left of C radial, isolated from anal sac; anal X pentagonal; anal sac not available. Arms of thick brachials, with U-sectioned ventral groove. Stem circular in section, strongly heteromorphic with alternating nodals and internodals of markedly different diameters, with rounded latus.

REMARKS. This material is preserved in medium to coarse sandstone, indicative of a higher energy environment than most Bokkeveld echinoderms which occur in the intervening shales. The two available slabs suggest considerable postmortem movement with most arms and stems disarticulated. However, no disarticulated cups are evident suggesting strong interplate sutures and/or cup shape less susceptible to disaggregation.

Family LECYTHOCRINIDAE Kirk,1934

Othozecrinus gen. nov.

TYPE SPECIES. *Othozecrinus royi* sp. nov.

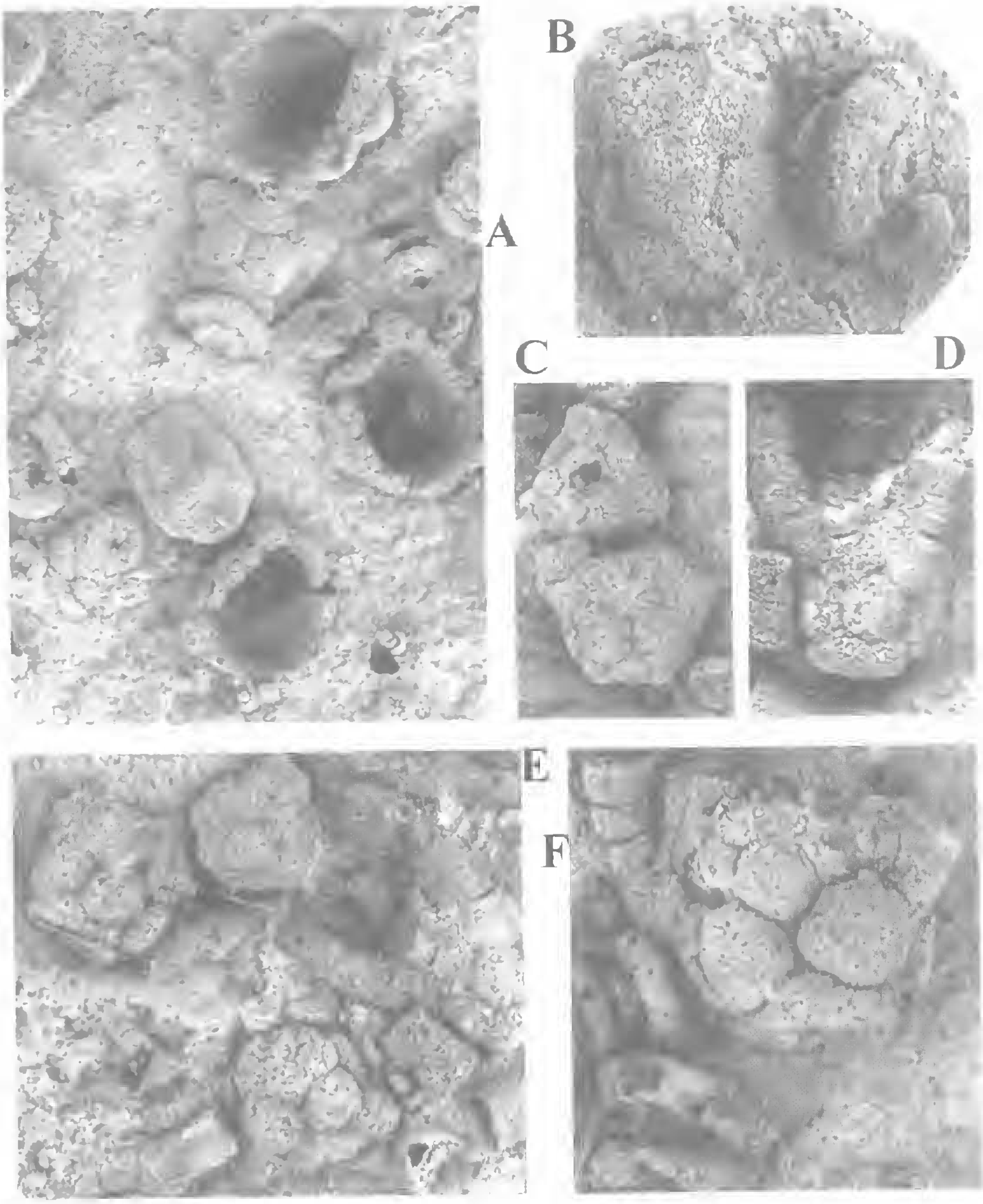


FIG. 28. *Thalamocrinus arenaceus* sp. nov. A, group of 6 cups, 3 of them looking into the cup, 2 looking at the base and 1 on its side B4538, ×3. B, cup in lateral view and dissarticulated macro and microcolumnals B4538, ×4. C, two cups in lateral view B4556D, ×3. D, cup B4556B, ×4. E, surface with 4 cups including that from D, all in lateral view B4556A, ×4. F, holotype crown showing posterior anal plates and part of an arm B4556C, ×5.

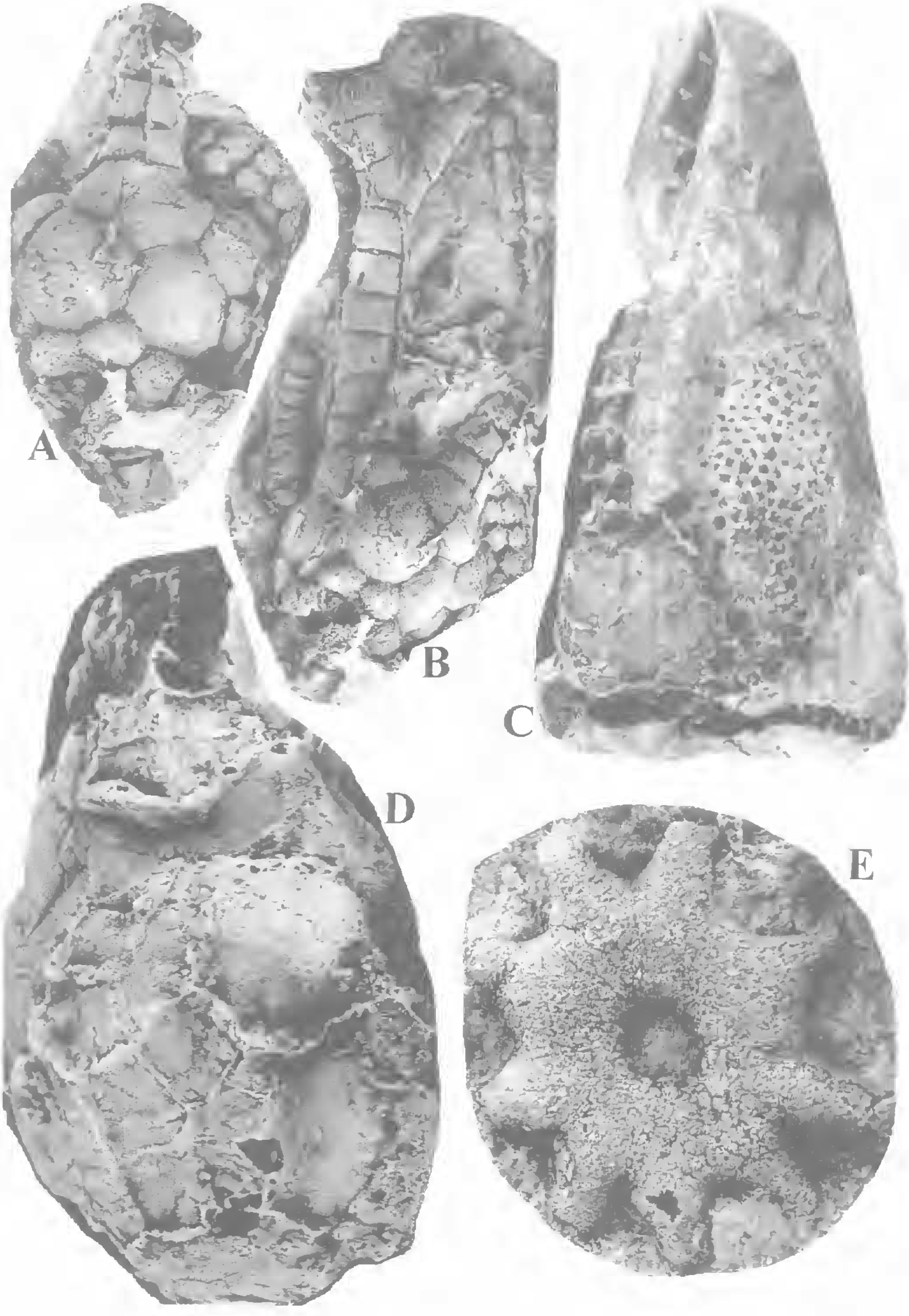


FIG. 29. *Othozecrinus royi* gen. et sp. nov. A-B, B4545, ×2 and ×1, respectively. C, internal mould showing large anal tube B4545, ×1. D, internal mould of cup SAM1169, ×3. E, stem columnal B4539A, ×4.

ETYMOLOGY. For Roy Oosthuizen, who collected much of the material described herein; an anagram to which is added only the 'cr'.

DIAGNOSIS. Cup wide bowl-shaped, with strongly convex plates; 5 infrabasals; radianal and anal X in cup in radial circlet. Anal sac of moderate length, inflated, of numerous large polygonal plates. Arms uniserial, branching isotomously; primibrach 7 axillary. Stem circular, relatively small diameter, with greatly expanded epifacet into 6-9 blunt spines.

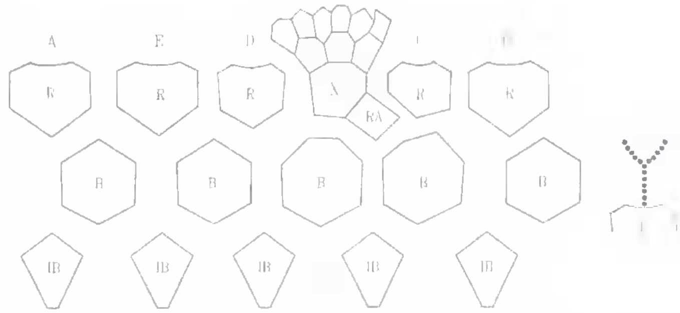


FIG. 30. *Othozecrinus royi* gen. et sp. nov., sketch of plate arrangement with arm branching as far as known on right and dotted lines on infrabasals indicating extent of stem facet. IB = infrabasal; B = basal; R = radial; RA = radianal; X = anal X; A-E above radials indicate rays.

REMARKS. While the details of this species are not entirely available, in particular the oral area and the branching pattern of the arms, it is sufficiently known to be confident it does not fit an existing genus. The two similarly sized (but differently shaped anal plates in the cup, convex infrabasals, 7 primibrachs and very distinctive stem combine to isolate this species. The Lecythocrinidae has members with 2 anal plates in the radial circlet. The anal plate arrangement of *Othozecrinus* is most similar (though not closely) to that of *Lecythocrinus* (cf Moore *et al.*,1978, fig.375.7) but the concealed infrabasals and the subquadrangular stem with large axial and 4 peripheral canals make close relationship unlikely. Other members of the family, *Cestocrinus* and *Corynecrinus*, have 0 or 5 anal plates in the cup and *Corynecrinus* has infrabasals concealed by the stem. The Euspirocrinidae is distinguished by its 3 anal plates in the cup and the Barycrinidae has a small radianal proximal to C radial. If forced to place this genus, with such distinctive stem, into a family it has to be the Lecytho- crinidae but that is a tentative assignment.

Othozecrinus royi gen. et sp. nov.
(Figs 29-31)

MATERIAL. HOLOTYPE: B4545 from Hex River Pass (C2S1, Gydo Formation). PARATYPES: SAM1169 from Boschluis Kloof (Gydo Formation), SAMK965 from Wolfaardt's Farm, Riet Valley, Ceres, B4524, B4539 from Grootrivier Hoogte (C2Q1, Gamka Formation), ROC20 Gamkapoort, Prince Albert at 33°18'S, 21°38'E (1st shale), ROL70 Warmwatersberg, Barrydale at 33°46'30"S, 20°55'30"E (1st shale). SUGD300 from De Doorns.B4600 from Platfontein in the Gydo Formation.

DIAGNOSIS. As for genus.

DESCRIPTION. Cup short, wide bowl-shaped, of thick, strongly convex plates. Infrabasals 5, forming pentagonal circlet, strongly convex, with short strong almost spinose projections on A, B and C infrabasals in larger specimens; stem facet central, hemispherical concavity, depressed distal to projecting convexity of infrabasals, with distinct rim. Basals 5, smooth, convex with sutures depressed, hexagonal (but with 2 proximal sides at very high obtuse angle) except heptagonal CD and BC basals. Radials 5, convex, with 1st primibrach narrower than radial; articulating facet slightly declined outwards, with strong transverse ridge and distinct muscle and ligament areas. CD basal supporting 2 anal plates, with right just proximal to left; distal edges of these 2 plates level with distal margin of radial circlet. Anal sac short, squat; polygonal plating apparently irregularly arranged, with finely scalloped edge to each plate indicating perforate wall, perforations circular along sutures. Arms uniserial, thick, of long brachials, with sharp deep ambulacral groove; primibrach 7 axillary; rest of arms unknown. Stem of large columnals (c. 15mm across not including blunt lateral spines), up to 4mm long, with small (up to 4mm diameter) central circular articulum, with up to 10 large blunt lateral spines. Articulum with small central lumen showing 5 rounded pits, one at each corner of the pentagon and circular jugulum centrally; rest of articulum with radial ridges and intervening grooves forming triangular segments, with fine peripheral rim to articulum. Latus (epifacet) with smooth gently convex (in radial direction) surface, extended into stout blunt spines; 6-9 blunt spines per

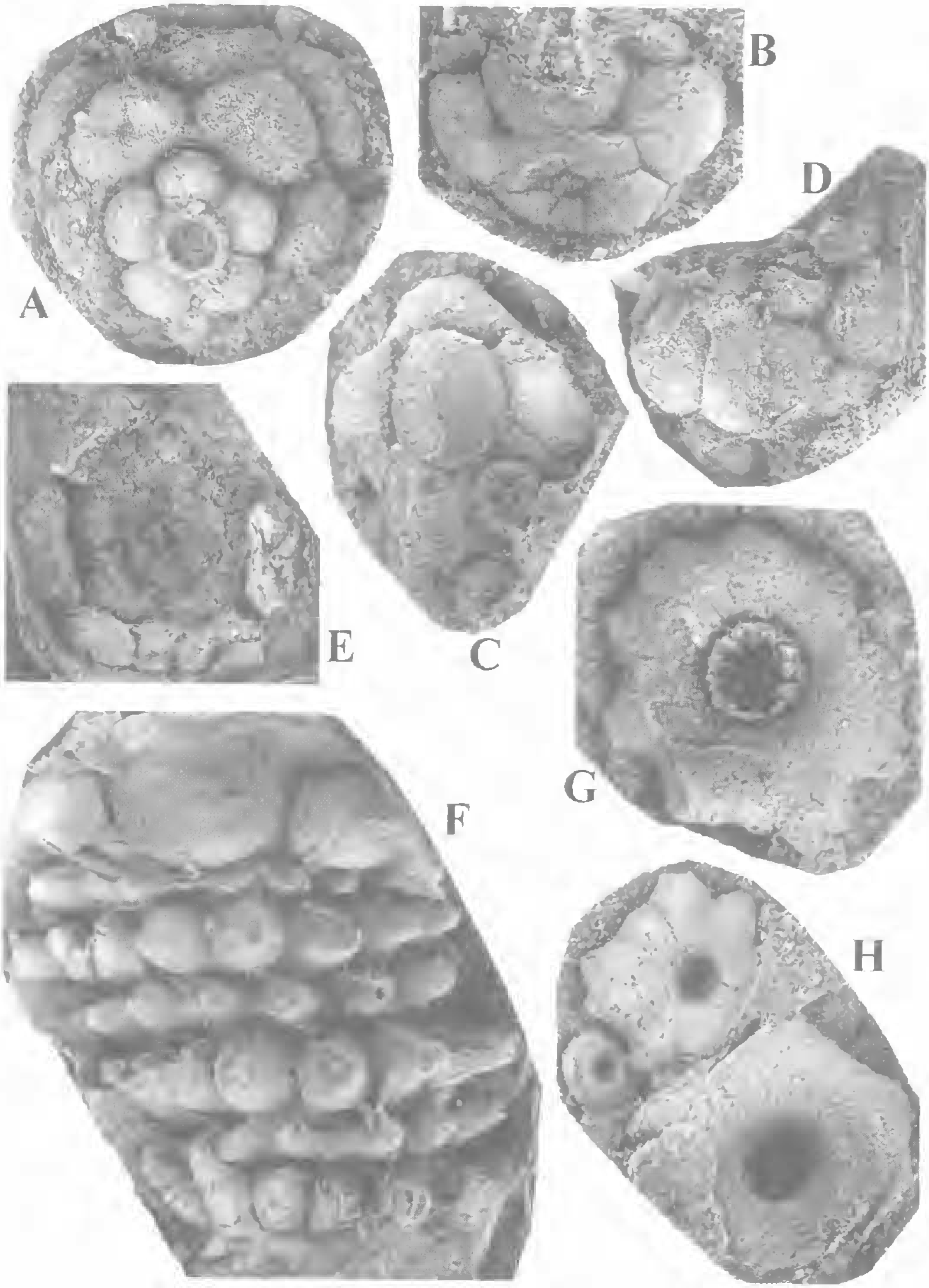


FIG. 31. *Othozecrinus royi* gen. et sp. nov. A. base of cup geol surv B4600, ×3. B. base of cup B4524, ×3. C. base of cup RO L70, ×3. D, lateral view of different cup RO L70, ×3. E, oral view of interior of cup SUGD300C, ×2. F. basal circlet with stem attached RO C20, ×3. G. columnal B4539B, ×5. H. columnals SUGD300A, ×3.

columnal. Blunt spines on every visible columnal in lateral view.

REMARKS. *Hyperexochus immodicus* Moore & Jeffords, 1968 from the Early Devonian of Tennessee has many lateral spines on its columnals and a small articulum but the surface of the articulum is differently ornamented and the spines are not in a single whorl, shaped differently and more numerous. *Sumaricystis radiatus* Stukalina, 1978 from the Middle Ordovician of the southern Tien Shan in central Asia is the most similar columnal but it has many more lateral spines and a narrow peripheral crenularium on the articulum. *Floricolumnus* Donovan & Clark, 1992 is similar in its greatly expanded epifacets which are almost spinose but in that genus they are well-separated nodals with smaller columnals between whereas in *Othozecrinus* they occur on each columnal evident (Fig. 31F). However, the central depression and narrow crenularium on both sides of these columnals indicate that at least one unexpanded columnal occurs between every pair of expanded ones. It seems unlikely that any of these genera is closely related to *Othozecrinus* and that the columnals with expanded epifacets have evolved independently in each case.

Class ASTEROIDEA de Blainville, 1830

Terminology and supragenerie classification largely follow Spencer & Wright (1966) except that: 1) their 'Mouth angle plate' (MAP) (='oral ossicles' of Blake & Guensburg, 1989) is here termed 1st ambulacral plate (AMB1) following Smith & Jell (1990); 2) their Amb1 is here termed ambulacral 2 following Bjork et al. (1968) and Smith & Jell (1990); 3) 'dorsal' and 'ventral' are used both for body and ossicle surfaces; 'adradial' and 'abradial' for directions toward and away from the arm axis, respectively; and 'proximal' and 'distal' for directions toward and away from the mouth, respectively. Dimensions of plates in the arms are indicated by: (rad.) = in radial direction or length of arm; (ad.-ab.) = in adradial-abradial direction across arm. In general, dimensions are referred to as 'long' and 'short' in the radial direction and 'wide' or 'narrow' across the arm.

Family PROMOPALAEASTERIDAE Schuchert, 1914

Aulacolatiaster gen. nov.

TYPE SPECIES. *Aulacolatiaster breviramus* sp. nov.

ETYMOLOGY. Latin *aulax*, furrow, *latus*, wide and *aster*, a star, referring to the wide ambulacral groove.

DIAGNOSIS. Arms 5, short (no longer than diameter of disc), wide. Dorsal surface with primary ossicular ring of large ossicles centrally. Ventral surface dominated by wide elliptical ambulacral grooves; ambulacrals wide, opposite, with extremely shallow ambulacral channel, with fine parallel ambulacral ridges running abradially parallel to plate margins and separating podial basins; 1st ambulacrals large, oriented vertically, paired across interradii; inferomarginals with pair of short lateral spines, becoming elongate proximally, isolating from the margin of the frame at least 1 narrow axillary (odontophore) in each interradius; adambulacrals with transverse row of extremely large prominent tubercles.

REMARKS. This genus is distinctive in its combination of meshwork dorsal plating in distinct radial columns, wide ambulacral groove with wide ambulacrals bearing fine parallel ridges separating podial basins, adambulacrals with row (ad.-ab.) of very large prominent tubercles and inferomarginals becoming wider proximally and each with 2 lateral spines. We consider it most closely allied to *Promopalaeaster* Schuchert, 1914 with which it shares the same type of dorsal plating, wide ambulacral groove, large 1st ambulacral, and interradial structure but from which it may be distinguished by its parallel ambulacral ridges indicating a single column of tube feet along each side of the arm, extreme size of the tubercules in a transverse row on the adambulacrals and short arms which could prove to be growth related when more material becomes available. Ambulacral ridge structure proximally distinguishes North American species, including the type species of *Promopalaeaster* but *Promopalaeaster elizae* Spencer, 1930 from the Upper Ordovician of Scotland and *Eoactis simplex* Spencer, 1914 from the Lower Silurian both exhibit (Spencer & Wright, 1966, figs 50.1 and 50.2e) ambulacral ridges parallel to each other and to the interplate sutures throughout as in *Aulacolatiaster*.

Aulacolatiaster bears some resemblance to *Palasterina* McCoy, 1851 in the wide ambulacral groove, parallel ambulacral ridges, and large 1st ambulacrals but is distinguished by its interradial structure and dorsal plating. Its placement will remain problematic until better preserved

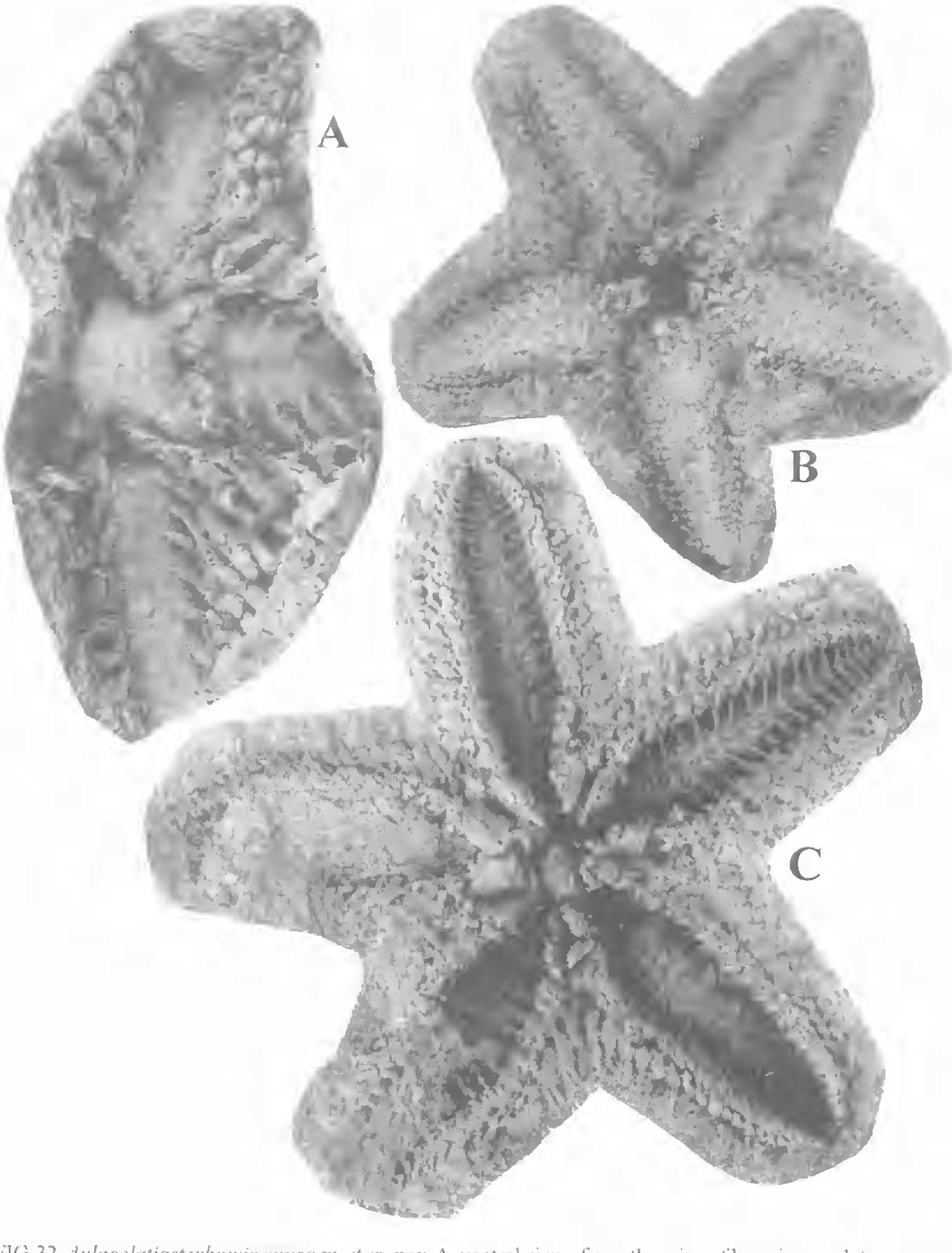


FIG. 32. *Aulacolatiaster breviramus* gen. et sp. nov. A, ventral view of mouth region of large incomplete paratype with mouth wide open SAMK1063, ×4. B-C, dorsal and ventral views, respectively, of holotype SAMK1018a & b, ×4 and ×6, respectively.

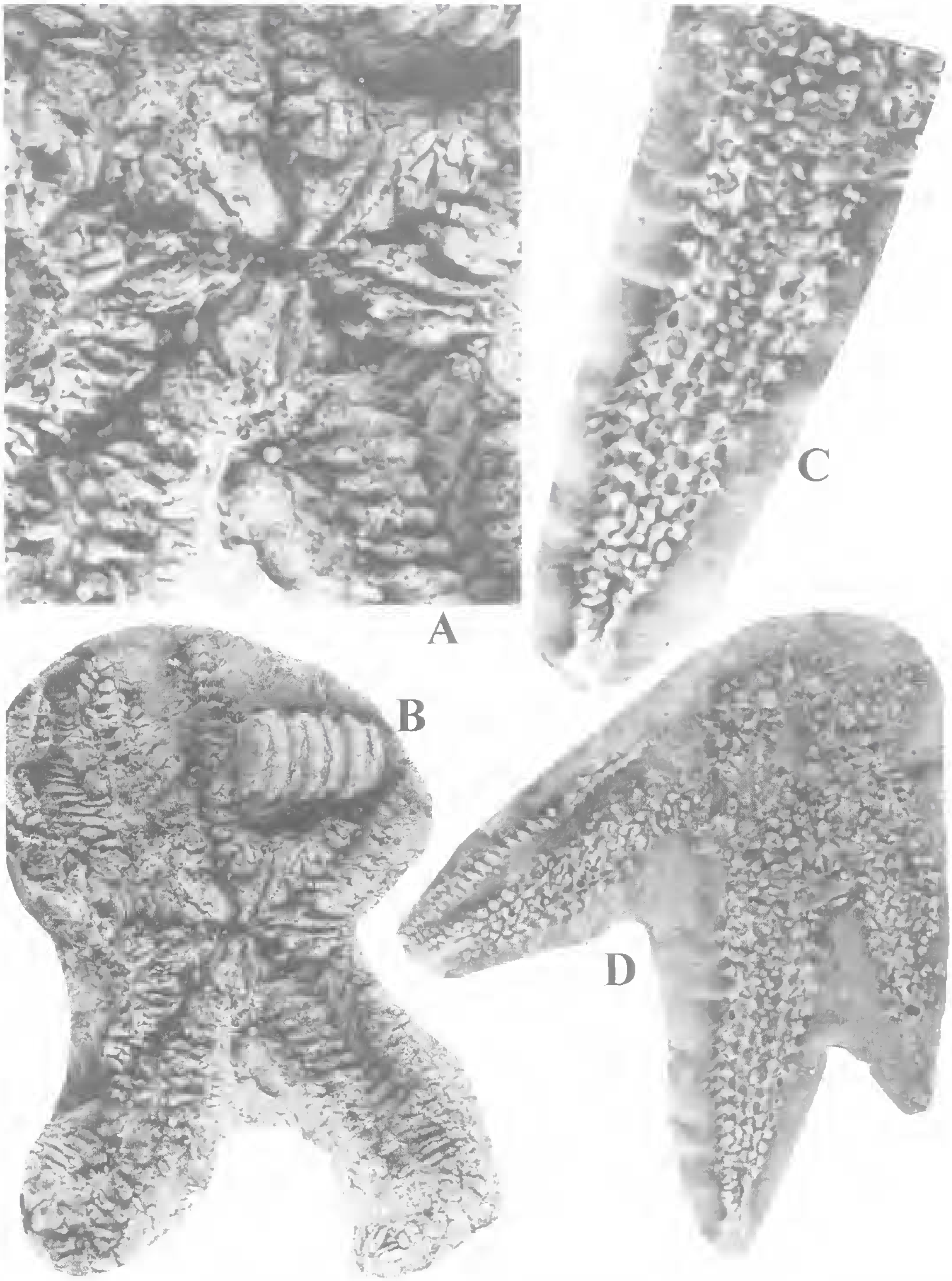


FIG. 33. *Ulrichaster macrodentatus* sp. nov. A-B, enlarged ventral view of oral region and ventral view of incomplete paratype with short section of crinoid stem in upper right RO 44, ×6 and ×3, respectively. C-D, enlarged dorsal view of arm and dorsal view of incomplete holotype PRV725, ×6 and ×4, respectively.

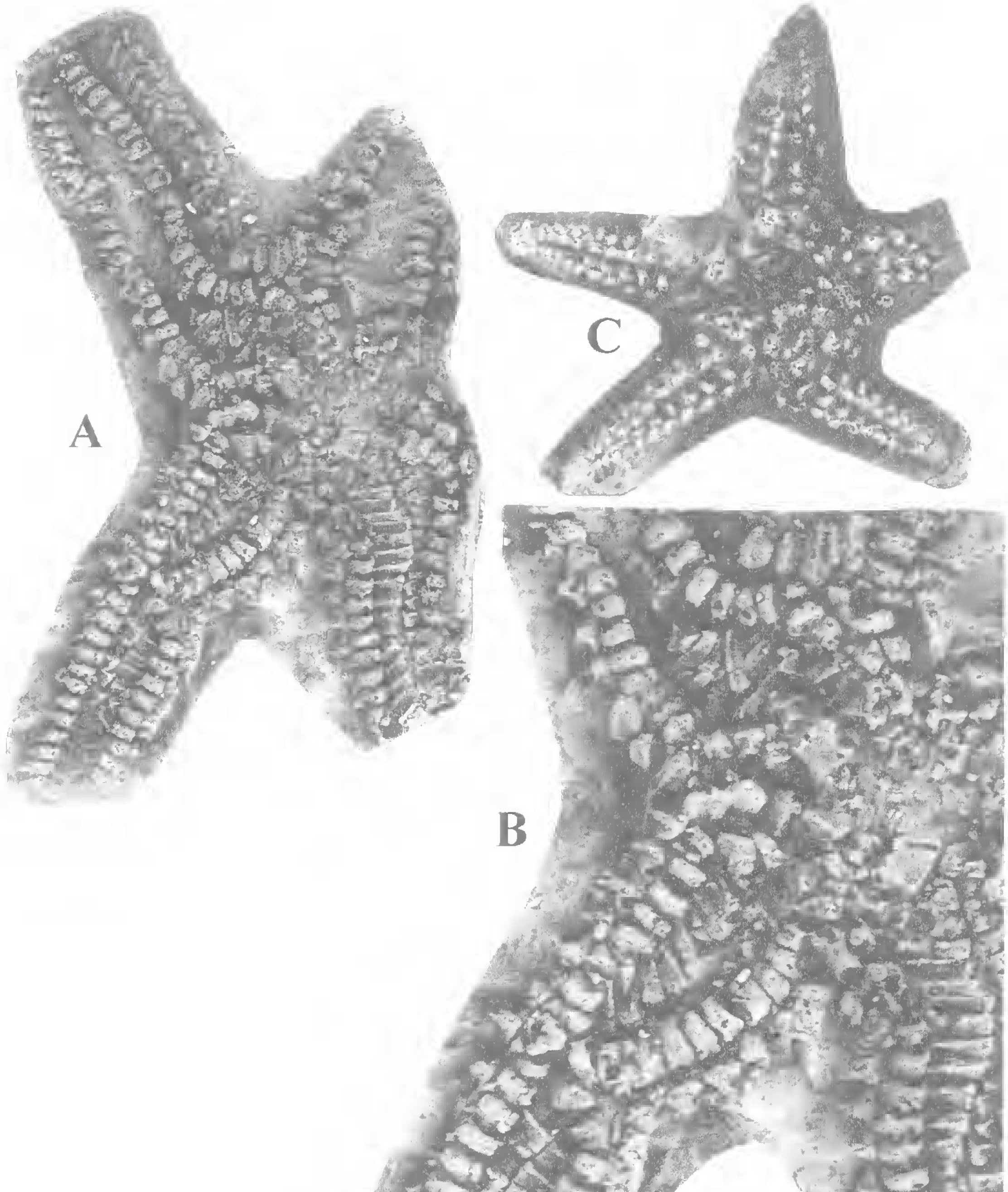


FIG. 34. *Ulrichaster macrodentatus* sp. nov. A-B, ventral view of slightly disarticulated paratype and enlargement of its oral area PRV737, ×5 and ×8, respectively. C, juvenile paratype in dorsal view PRV738, ×10.

material becomes available, particularly a dorsal surface.

Aulacolatiaster breviramus sp. nov.
(Fig. 32)

ETYMOLOGY. Latin *brevis*, short and *ramus*, arm; for the relatively short arms.

MATERIAL. HOLOTYPE: SAMK1018, dorsal and ventral external moulds from Riet River, N of Ceres Division on Wupperthal Road; S side of farm which is also called Groot Rivier in the neighbourhood; Gydo Fmn, 33m below top of unit. SAMK1063 incomplete ventral external mould from Wolfaardt's Farm near Ceres, about 100m NNE of the house.

DIAGNOSIS. As for genus.

DESCRIPTION. Stellate. Arms 5, short (10mm from oral axis to arm tip on holotype), wide (4mm at widest point). Dorsal surface with primary ossicular ring of large ossicles in radial positions and with central pit or perforation on each, outlines unclear but apparently subquadrate; a further circlet of large ossicles probably present in interradial positions and resting on the circlet of radially disposed ossicles (single dislocated subrectangular plate lying in interradial position (Fig. 32B); dorsal surface of arms with broad median groove (probably preservational), with midline bordered by columns of weakly tuberculate plates that abut along the midline of the arm, with at least 3 columns of tuberculate plates abradially separated by deep pits (suggesting some sort of meshwork stucture but this remains unclear from the available specimen), with columns of plates laterally aligned into rows across the arm, without clearly defined superomarginals. Ventral surface with small interradii and wide elliptical arms; ambulacral grooves elliptical, occupying about 2/3 arm width for most of arm length (more than 80% distally), extending to arm tip; ambulacrals wide, opposite, with extremely shallow median ambulacral channel; ambulacral ridges fine, parallel, with very small expansion at adradial end, running abradially parallel to plate sutures (this attitude not absolutely certain but where sutures between successive ambulacrals are evident they are parallel to the ridge), weakly expanded at abradial end to about same length as adambulacral; 1st ambulacrals large, plough shear-shaped, oriented vertically, paired with convex sides adjacent across interradii; inferomarginals wider than long, becoming much wider proximally with at least 1 axillary (and possibly 3 or 4) separating adambulacrals from inferomarginals in each interradius, with pair of short lateral spines directed abradially on each inferomarginal; adambulacrals with transverse row of prominent tubercles (tubercles may be irregularly arranged in smaller individual but well aligned in transverse rows from expanded abradial end of ambulacrals in large individual (Fig. 32A))

REMARKS. The holotype is known from external moulds of both surfaces but whereas the ventral mould is very well preserved the dorsal mould seems to have been abraded (probably since collection) and does not preserve much detail. The fragmentary external mould of the ventral oral area of a larger individual is well preserved but only a small fragment. Both casts of the ventral surface have a convex mound of matrix in the oral pole suggesting that the central dorsal structure was weak and collapsed easily upon death. Well-developed podial basins between the ambulacral ridges abradially are shared by contiguous ambulacrals but preservation is not good enough to determine whether or not a pore passes through the basin floor.

Family URASTERELLIDAE Schuchert, 1915

Ulrichaster Spencer, 1950b

TYPE SPECIES. *Urasterella ulrichi* Schuchert, 1915 from the Middle Ordovician of central USA.

REMARKS. Spencer (1950b) subdivided *Urasterella* McCoy into a group with a single row of ossicles in the dorsal midradius of the arms (further subdivided on features of dorsal arm ossicles between the radial and marginal columns) and a second group with 2 rows of ossicles in the dorsal midradius (i.e., on either side of the arm axis). He erected *Ulrichaster* for the latter group which accepts the new species described herein.

Ulrichaster macrodentatus sp. nov.
(Figs 33, 34)

ETYMOLOGY. Greek *macros*, long and *dentatus*, tooth; for the long 1st ambulacrals.

MATERIAL. RO44 from the Voorstehoek Shale (C2S2) at 33°30'S; 19°49'E near Matroosberg, Worcester (Hex River Pass). PRV738, 737 (and counterpart PRV725) from Tafelberg in the Waboomberg Shale (C2S4).

DIAGNOSIS. Dorsal surface with very open meshwork of ossicles in radial columns, columns symmetrical about arm axis. 1st ambulacrals large, elongate, reaching interradial margin or

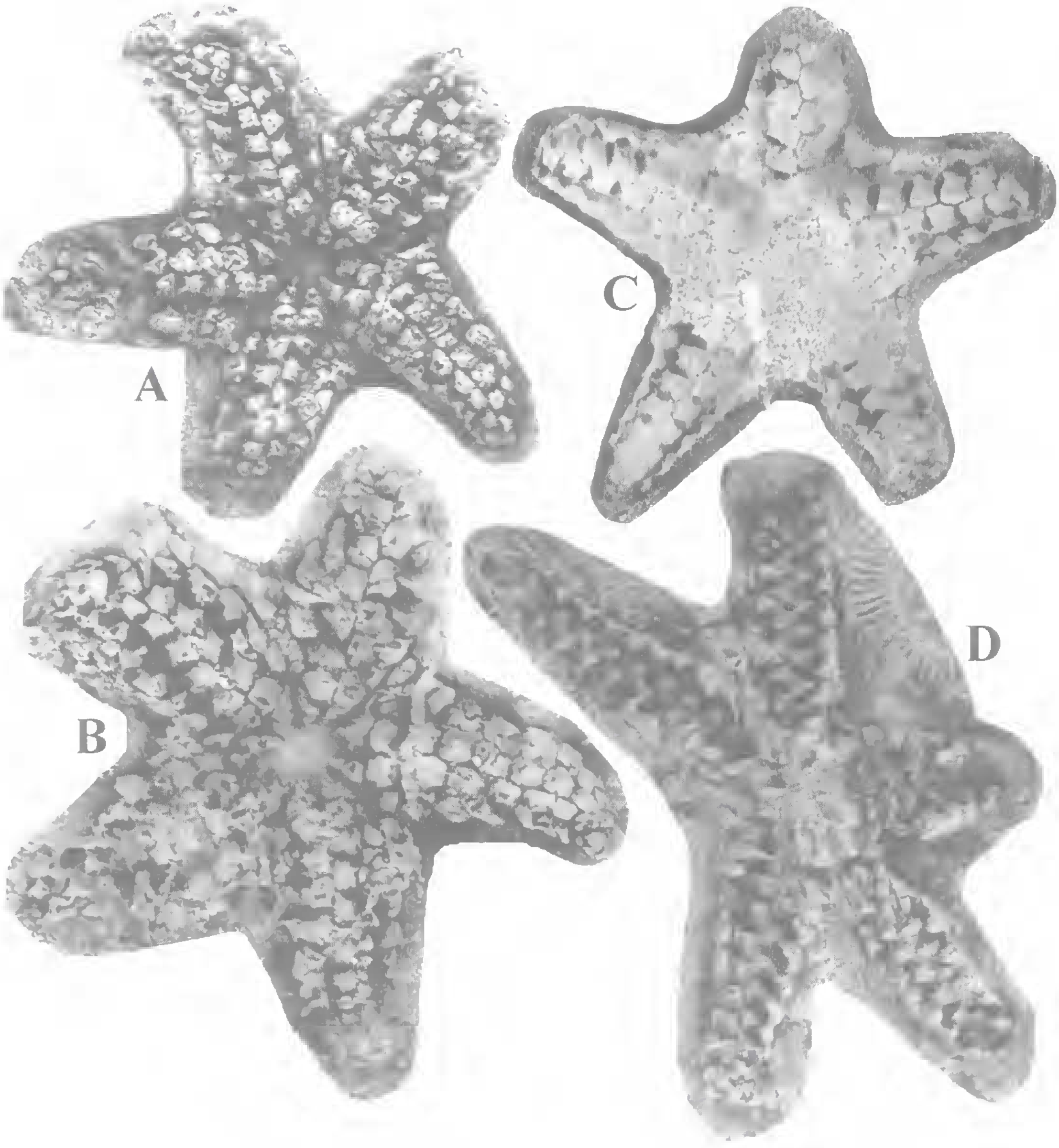


FIG. 35. *Haughtonaster reedi* Rilett, 1971. A-B, ventral and dorsal views of juvenile holotype SAM 3881, ×5. C, dorsal view of juvenile paratype SAM3375, ×5. D, ventral view of SAM K978, ×6.

close to it, in closely adjacent pairs across interradii.

DESCRIPTION. Stellate. Arms 5, long (at least twice disc diameter). Dorsal surface an ordered meshwork (with large perforations) of small tuberculate elongate plates in 4 radial columns (2 columns on either side of arm axis smaller than next columns abradially) linked by less regular struts in transverse rows, without obviously differentiated primary ossicular ring or other plates (but disc plating not clear on available specimens). Ventral surface with long parallel sided ambulacral grooves; ambulacrals wide, opposite, with diagonal ambulacral ridges having curved ventral edges forming basins abradially.

1st ambulacrals large, extending to interradial margin, straight but with strong lateral projection on adradial side, paired across interradii; adambulacrals narrow, subrectangular to subdiscoidal in ventral view, without spines; inferomarginals forming lateral margins of arms, small (same size as abradial dorsal plates), with 1 or 2 or more short stubby spines forming spinose margin.

REMARKS. None of the available material is well preserved but enough is available to show the features of *Ulrichaster* in particular the short stubby spines of the inferomarginals and abradial dorsal plates and the ordered meshwork of radial columns of the dorsal plating with 2 columns either side of the arm axis. However, shape of the 1st ambulacrals and the larger pits between dorsal plates distinguish it from other members of the genus. The type species, *U. ulrichi* has more columns of ossicles covering the arm dorsally and does not appear to have the larger pits of the dorsal meshwork as in *U. macrodentatus*. *U. gutterfordensis* Spencer, 1918 has small 1st ambulacral plates. *Salteraster biradialis* Withers & Keble, 1934 from the Ludlow of Victoria (included by Spencer (1950b) in *Ulrichaster*) is an ophiuroid with the 2 median rows of ossicles the dorsal side of the ambulacrals, any dorsal plating having been removed or not preserved.

Class OPHIUROIDEA Gray, 1840
Order STENURIDA Spencer, 1951
Suborder PAROPHIURINA Jaekel, 1923
Family EOPHIURIDAE Schöndorf, 1910

Haughtonaster Rilett, 1971

TYPE SPECIES. *Haughtonaster reedi* Rilett, 1971 from the Gydo Formation near Ceres.

DIAGNOSIS. Disc pentagonal, dorsal surface of smooth oval plates surrounded by an irregular mass of very fine, almost spicular elements; ventral interradii triangular, with polygonal plates having some perforations on sutures (i.e. a few oppositely scalloped margins of plates). Ambulacrals offset across arm axis, rectangular in dorsal view; adambulacrals wide and gently oblique to arm axis in ventral view, forming lateral walls of arm; podial basins subcircular, very deep. 1st ambulacral with strong curved ridge forming distinctive elliptical basins interradially.

REMARKS. Rilett (1971) assigned this genus to the Eophiuridae to which Spencer & Wright (1966) assigned only *Eophiura* from the Arenig of Czechoslovakia. The more mature specimens now available indicate that a close relationship is unlikely although the 2 genera should probably be retained in the same suborder. Hotchkiss (1976) established a subordinal level division of the Stenurida based on whether ambulacrals were opposite or offset across the arm axis, noting that pre-existing classification had been based on grades of development and inferring that the development of offset ambulacral columns indicates a monophyletic clade of Palaeozoic ophiuroids. He erected the Scalarina for stenurids with opposite ambulacrals and the Parophiurina is available for those with offset ambulacrals. Phylogeny within the Paraophiurina is not clear and would require a review of known members, which is outside the scope of this paper. *Haughtonaster* is distinctive in that suborder in lacking spines on the arms, lacking a column of sublateral plates, in its long slender tapering arms, in its deep circular podial basins and in its wide adambulacrals enclosing the arm laterally. In the shape of ambulacrals along each arm, nature of adambulacrals and podial basins, and in particular the distinctive ridge on the 1st ambulacral, *Haughtonaster* very much resembles *Stenaster* Billings, 1858. However, that genus belongs to the Scalarina and a close relationship would not be possible unless the offset arrangement of ambulacrals evolved more than once. We do not speculate on that possibility and retain *Haughtonaster* in the Parophiurina. Because we can see no workable family arrangement we retain Rilett's (1971) family assignment.

Haughtonaster reedi Rilett, 1971
(Figs 35-37)

MATERIAL. HOLOTYPE: SAM3881 from Hottentots Kraal. PARATYPE: SAM3375 from Hottentots Kloof, Ceres. OTHER MATERIAL: ROC50, RO122, RO804 from Gamkapoort, Prince Albert at 33°18'S, 21°38'E in the Gydo Formation; B4567 from Swaarmoed Pass, 1.3 miles from Great Swaarmoed Farm, Ceres; PRV1484, SAM13472 from Voetjies Kloof Suid; SAM13470; SAMK1016 from Riet River (also called Groote Rivier) N of Ceres Division on Wupperthal Road, S side of farm in Gydo Formation; SAMK978 from Wolfaardt's Farm near Ceres (100m NNE of house).

DESCRIPTION. *Overall form.* Maximum radius 7-30mm, disc radius 5-6mm. Arms 5, short and blunt in small specimens, in large specimens weakly petaloid in proximal 1/2 and strongly tapered over distal 1/2, with elongate pointed tip. Disc pentagonal, extending to 5th or 6th

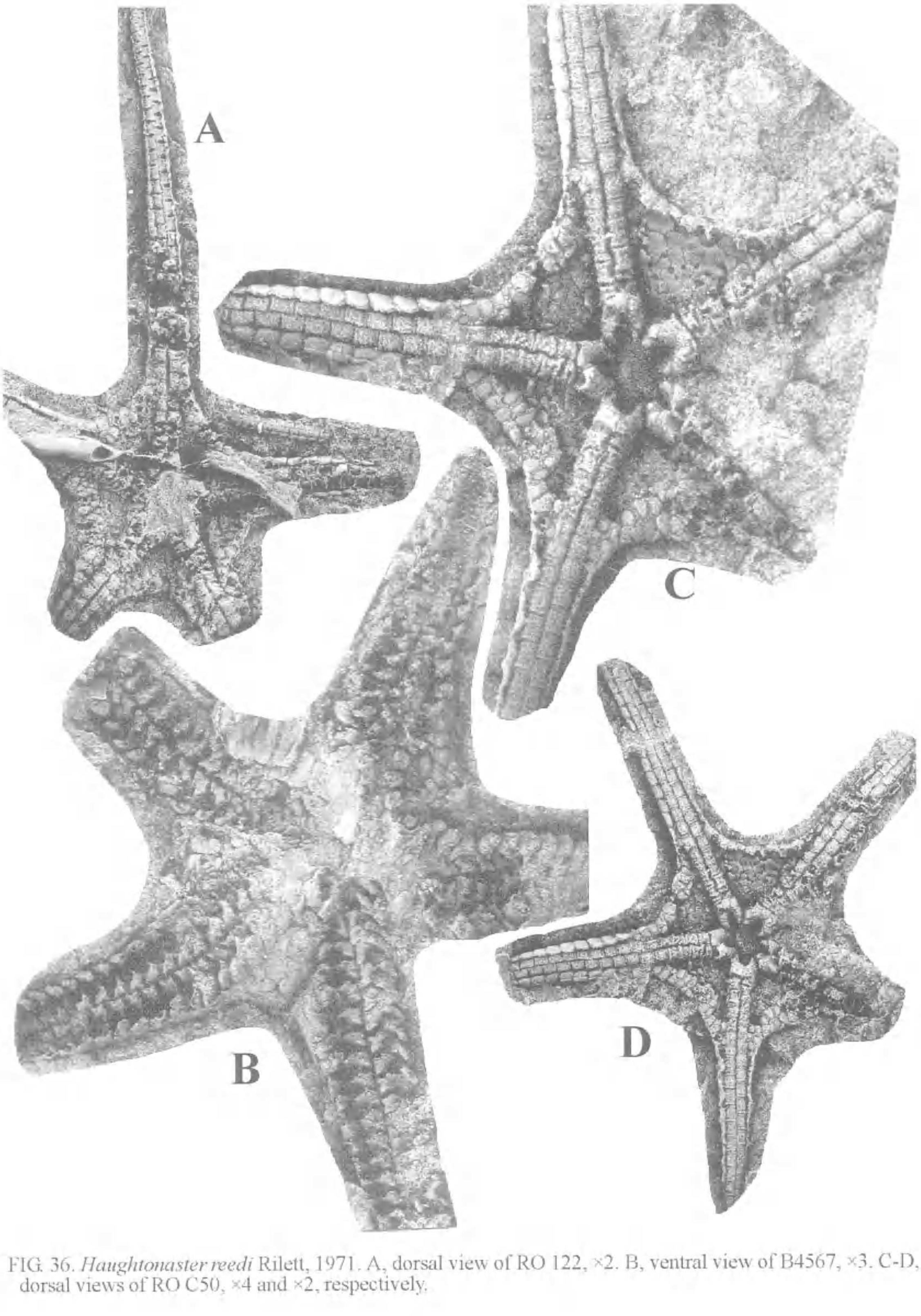


FIG. 36. *Haughtonaster reedi* Rilett, 1971. A, dorsal view of RO 122, ×2. B, ventral view of B4567, ×3. C-D, dorsal views of RO C50, ×4 and ×2, respectively.

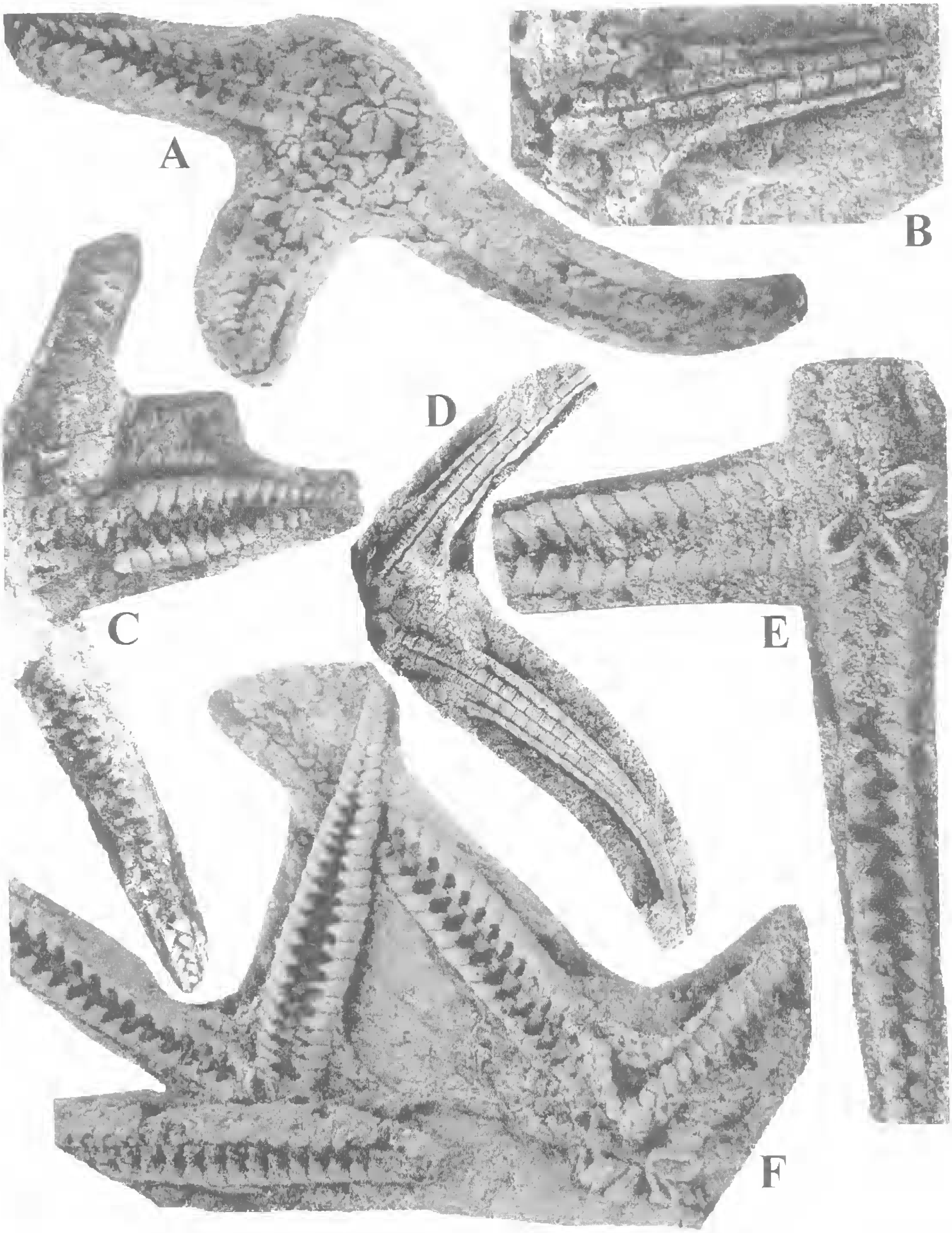


FIG. 37. *Haughtonaster reedi* Rilett, 1971. A, ventral view of incomplete smaller specimen RO 804, ×6. B, dorsal view of proximal part of arm RO C50 ×4. C, ventral view of incomplete adult SAM13472 ×3. D, dorsal view of incomplete adult RO C50 ×2. E, ventral view of incomplete adult SAM13470 ×4. F, ventral view of 2 adults PRV 1484 ×4.

ambulacral; in small specimens only 3-4 tiny plates in interradius, in larger specimens 8-12 polygonal plates in a triangular interradius, plates irregularly polygonal, possibly disc plates with scalloped margins in larger specimens (no area of plating well preserved). Only small fragments of dorsal disc available.

Arm plating. Ambulacrals in dorsal view subquadrate (in smaller specimens) to subrectangular (larger specimens), offset across arm axis distal from 2nd ambulacral, with sharp elliptical clefts between successive ambulacrals in each column, with weakly zigzag (obtuse projection at midlength of ambulacrals pointing at recessive interambulacral suture in opposite column of ambulacrals) line of suture between the 2 columns in arm axis. Ambulacrals in ventral view subtrapezoidal, separated from succeeding ambulacral in same column by shallow rounded basin shared by 2 ambulacrals (i.e. interambulacral suture runs through middle of depression) and descending abradially into deeper part of podial basin, with straight radial axis between 2 ambulacral columns; ambulacral channel very shallow, barely discernible. Adambulacrals in dorsal view subtriangular, extending ventrally to form the abradial wall of the arm, with adradial tip directed at proximal end of ambulacral. Adambulacrals in ventral view wide, with parallel interadambulacral sutures, continuing abradially to form lateral wall of arm, without spines, with sharp adradial projection between podial basins. Podial basins subcircular with slight expansion on adradial side between adjacent ambulacrals, extremely deep adjacent to adambulacrals and shallower adjacent to radial axis of arm, apparently with some subtle ledges and dimples on the evenly curved walls (but preservation is not good enough to be certain of consistent structures).

Mouth frame. Dorsal aspect not available except in small specimen: central circular dorsal depression but plating details not available. Mouth small; no buccal slit. Smallest specimen with 1st ambulacral unspecialised except for slight proximal projection. 1st ambulacral becoming more elongate (radially) with growth, developing strong curved ridge convex towards arm axis; curved ridges from adjacent arms forming distinctive elliptical basins interradially.

REMARKS. The marked changes that take place in this species during growth involving increasing arm length relative to width and development of the pentagonal disc could be considered indicative of separate species if it were not for the distinctive structure of the 1st ambulacrals and the broad adambulacrals forming the lateral walls of the arms that link the specimens over the whole size range. There is no discernible variation in the available material of the same size. As discussed under the generic remarks above the only species deserving of comparison is *Stenaster obtusus*, which has its ambulacrals opposite each other.

Ophiuroid arm indet. A
(Fig. 58A)

MATERIAL. SAMK625 from Gamkapoort.

DESCRIPTION. This specimen, preserved only as an external mould, is interpreted as the ventral aspect of a part of a free arm with the 2 alternating columns of vaguely hexagonal ambulacrals on the right, serving to identify the slightly zigzag arm axis; proximal is inferred as up the page from the gradually diminishing size of plates in the opposite direction (distal); a column of transverse plates abutting the ambulacrals laterally is interpreted as a column of sublaterals; the column of longitudinally elongate plates forming the lateral margin of the arm (and to which the abradial end of the sublaterals abut at the junction between successive plates) is interpreted as the lateral column and is not obviously spinose. The subquadrate depressed areas bordered by the ambulacral and lateral columns and separated by the sublaterals (podial basins?) are fully floored and have 2 distinct depressions on that floor; one is adjacent to the distal end of the ambulacral and the other is proximal and abradial against the lateral plate.

REMARKS. Structure of the arm with 3 columns of plates (ambulacrals, sublaterals and laterals) suggests a primitive ophiuroid among the Stenurida (cf. *Eophiura*, *Pradesura*, *Stuertzaster* etc.). The alternating columns of ambulacrals exclude it from Hotchkiss's (1976) Scalarina and place it in the Parophiurina as used herein. However, there is no comparable form in this or any related group. Other stenurids with alternating ambulacrals may have the podial basin entirely on the ambulacrals (*Eophiura*, *Pradesura*) or have very wide podial basins (*Stuertzaster*) but none have the subquadrate podial basins of this South African form. This specimen represents a new genus but provides insufficient information for its definition forcing us to retain it in open nomenclature. The position of the sublaterals forming the proximal margin of

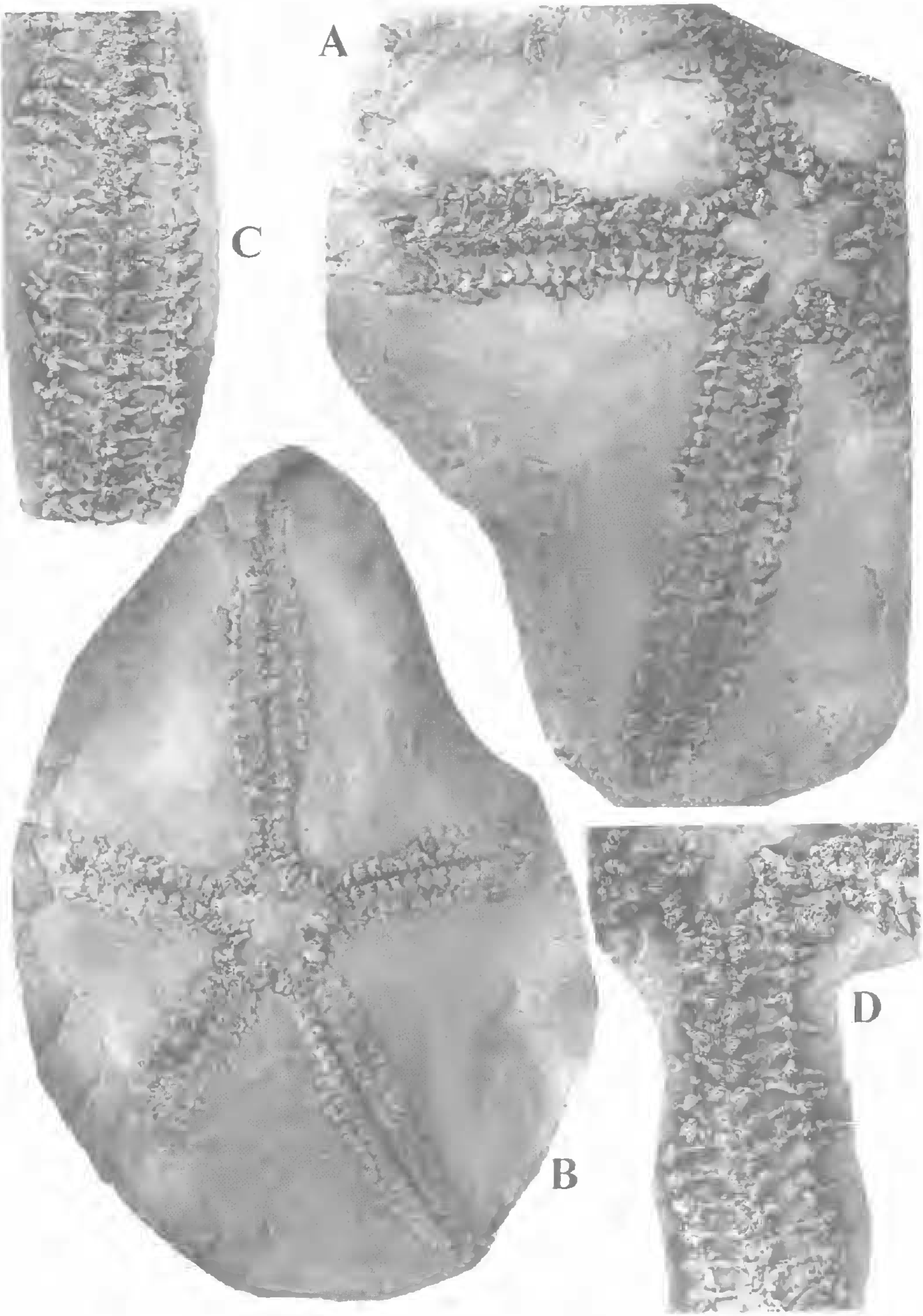


FIG. 38. *Hexuraster weitzi* (Spencer, 1950a), lectotype, SAM11055. A. ventral view (mould and thus latex cast incomplete) ×1.5. B. dorsal vie ×0.9. C-D, enlargements of parts of arms from A in ventral vie ×2.5.

the podial basin suggests a possible affinity with *Stuertzaster,* which is as much as can be said at the moment.

Order OEGOPHIURIDA Matsumoto, 1915
Suborder LYSOPHIURINA Gregory, 1896
Family CHEIROPTERASTERIDAE Spencer, 1934

Hexuraster gen. nov.

not *Hexura* Simon, 1884: 314.
Hexura Spencer, 1950a: 300.

TYPE SPECIES. *Hexura weitzi* Spencer, 1950a from the Lower Devonian of South Africa.

DIAGNOSIS. Body large (incomplete holotype 130x80mm); disc uncalcified, extending to arm tips. Arms slightly petaloid. Ambulacrals cylindrical with lateral projection (or toe of boot) shorter than radial length. Adambulacrals wide (ad-ab), expanded abradially to be T-shaped, with single very strong lateral spine on each adambulacral. Madreporite interradial, close to mouth frame on ventral surface. Mouth frame small for size of animal, plates not massive, with well-developed podial basin on 2nd ambulacral. Mouth large, with short buccal slit between 1st 2 ambulacrals.

REMARKS. Spencer's (1950a) name was preoccupied by a spider genus so the replacement name is proposed herein. Spencer (1950a, figs 1 - 3 - 4) included 3 specimens which are assigned herein to 3 different genera. Jell (1997) chose SAM11055 (Spencer, 1950a, figs 1,2) as lectotype of *H. weitzi* and placed it in the Cheiropterasteridae which he reinstated from synonymy with the Encrinasteridae (Spencer & Wright, 1966). Spencer (1950a) allied *Hexuraster* with his Euzonosomatidae (=Encrinasteridae of Spencer & Wright, 1966) and although he quoted several reasons that do not apply to the lectotype of the type species but rather to his figs 4 and 5 we consider the Cheiropterasteridae closely related to the Encrinasteridae. Following Jell (1997), the family is known from the Early Devonian of Germany and South Africa and the Early Carboniferous of Indiana.

Hexuraster weitzi (Spencer, 1950a)
(Figs 38, 39)

Hexura weitzi Spencer, 1950a: 300, figs 1, 2 (not figs 3-5).

MATERIAL. LECTOTYPE: (chosen Jell, 1997) SAM11055 (130×80mm) from the Lower Devonian Bokkeveld Series, at De Doorns; RO45 (about 30mm diameter) from the Gydo Formation at Gamkapoort, Prince Albert, 33°18'S, 21°38'E.

DIAGNOSIS. As for genus.

DESCRIPTION. *Overall form.* 5-armed, preserved radius 15-65mm, arm radius just greater than disc radius. Arms slightly petaloid, with rounded only weakly tapered tips. Disc very large, uncalcified, extending to arm tips, with high obtuse angled re-entrant in some interradii but continuing almost circular in other interradii.

Arm plating. Ambulacrals subquadrate in dorsal view, offset across arm axis distal from ambulacral 3, boot-shaped in ventral view, with narrow cylindrical leg, long lateral process (foot) having a slight concavity on proximal side (instep) to receive abradial tip of distal end of next proximal ambulacral. Ambulacral channel prominent, formed by half grooves along the adradial edge of each ambulacral, with straight line of suture between 2 ambulacral columns in bottom of amulacral channel. Adambulacrals with long lateral projection abutting against the toe of ambulacrals; in dorsal view abradial subtrapezoidal expanded part of adambulacral with sharp proximal-distal ridge aligned on all adambulacrals to form ridge along the length of arm; ridge sharper on adradial side than on abradial side, with furrow on abradial side; lateral face subcircular to oval, flat, with single stout lateral spine attached apparently by suture. In ventral view expanded head of adambulacral subcircular, with low proximal-distal ridge aligned along the arm into one long ridge.

Madreporite. Subcircular to oval, large (4mm max. diameter in lectotype), possibly with vermiform ornament (not entirely clear in lectotype), situated only slightly asymmetrically interradially adjacent to ambulacral 2.

Mouth frame. Mouth very large in available specimens, with 1st ambulacral situated interradially leaving large embayments in each arm axis. 1st ambulacral long and narrow with deep transverse groove near midlength in dorsal view, similarly shaped but without transverse furrow in ventral view, with sutured junction to 2nd ambulacral almost radial. Smaller specimen with smooth basin-like recess under distal part of 1st ambulacral. 2nd ambulacral little different from more distal ambulacrals, subquadrate, indistinct in dorsal view, subquadrate, with well-developed podial basin in ventral view.

FIG. 39. *Hexuraster weitzi* (Spencer, 1950a), incomplete juvenile in ventral view RO 45 -4.

REMARKS. The lectotype has some iron oxide minerals deposited in the external mould obscuring details in some areas, particularly in the mouth frame but details of the arms are available by reference to different parts of the mould.

Family ENCRINASTERIDAE Schuchert, 1914

Encrinaster Haeckel, 1866

not *Aspidosoma* Fitzinger, 1843.
Aspidosoma Goldfuss, 1848: 145; Schöndorf, 1910: 4
Encrinaster Haeckel, 1866:67; Lehmann, 1957: 28; Spencer & Wright, 1966: U85
Euzonosoma Spencer, 1930: 411, Spencer & Wright, 1966: U86, Lehmann, 1957: 24

TYPE SPECIES. *Aspidosoma arnoldi* Goldfuss, 1848 from the Lower Devonian of Germany.

SPECIES ASSIGNED. *arnoldi*, *tischbeinianus*, *petaloides*, *eifelensis*, *goldfussi*, *pontis*, *roemeri*, *schmidti* and *laevidiscus*.

REMARKS. The several German species of this genus were reviewed by Schöndorf (1910) (as *Aspidosoma*) and Lehmann (1957). Spencer (1930) spread these German species and others from Britain and North America between *Encrinaster* and *Euzonosoma*. Generic placement of *tischbeinianus* depends on the concepts of these 2 genera.

Spencer (1930: 404) provided a key for genera of his Euzonosomatidae, a junior synonym of Schuchert's Encrinasteridae, in which he indicated the 'Geno-holotype' of *Euzonosoma* as *E. petaloides* (Simonovitsch). In the same work (1930, 411) he appears to have tried to designate a different genotype in the sentence '*Euzonosoma orbitoides*, n. sp., is chosen as the holotype of the species'. Although his intention is not clear from this work, the first of these citations links the words genus (geno-) and type (holotype) and must be accepted as a valid designation of a type species. The second citation does not link the words 'genus' and 'type' in any way and cannot be considered a valid designation of a genotype or type species. Therefore, the type species of *Euzonosoma* is *Aspidosoma petaloides* Simonovitsch, 1871 by original designation.

No action by any subsequent author can change this designation. Even subsequent action by the original author (e.g., Spencer & Wright, 1966) cannot supplant the original designation. So regardless of Spencer's intentions, which may be inferred from his subsequent citation of *E. orbitoides* as the type species and despite subsequent workers acceptance of *E. orbitoides* as type, *E. petaloides* must be considered the type species. This recognition should not greatly change the concept of *Euzonosoma* because Spencer (1930: 404) included that species in his generic concept.

Spencer (1930) distinguished between these 2 genera in his key by only 1 feature, the degree of widening (ad-ab) of the adambulacrals in the median regions (i.e., midlength) of the arm: in *Euzonosoma* the adambulacrals are distinctly broader in the median region than at the extremity whereas in *Encrinaster* adambulacrals are only slightly differentiated (inferring some widening but only slight) compared to the extremity. The variation usually comes down to width of the adambulacrals within the disc as opposed to their width just outside the disc. Most authors and

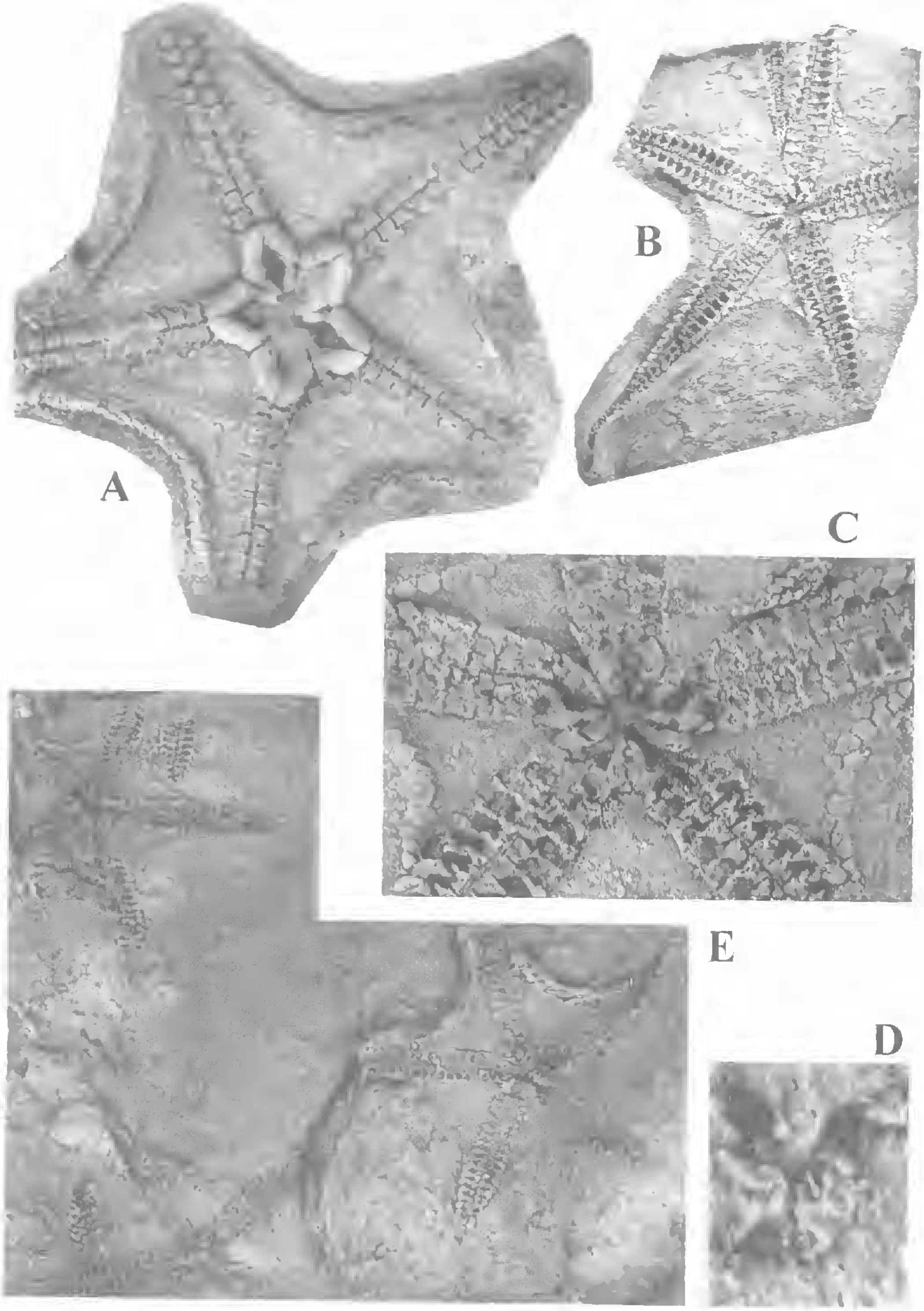


FIG. 40. *Encrinaster tischbeinianus* (Roemer, 1862). A, dorsal view of SAM K1018 ×2. B-D, ventral view of whole specimen, of disc area and of madreporite, respectively. SUG299, ×1.2 ×3.5 an ×15, respectively. E, slab with 3 individuals in ventral vie ×0.8 (figured by Spencer, 1950, figs 4, 5).

particularly Spencer accept that ambulacrals and adambulacrals could rotate in a transverse direction (ab.-ad.) and this is reflected in width of the ambulacral groove which varies from specimen to specimen. We suggest that such rotation is gretly restricted in the disc but not so restricted in the free arms. Therefore, we suggest that the specimens with wide adambulacrals in the proximal free part of the arm are ones where the adambulacrals have rotated laterally to expose their full width in dorsal view. Thus width of adambulacrals in direct dorsal or ventral view may often be influenced by the attitude in which a specimen is buried (i.e., whether adambulacrals are curled ventrally concealing much of the ambulacrals or flattened out on the sediment and often dislocated from the ambulacrals. In some instances, particularly where preservation is in fine mudstone, the degree of convexity of the arm is greater where the adambulacrals appear narrow and least where the adambulacrals appear widest; this suggests to us that rotation of the plates in the arm is a highly significant factor in determining the dorsal appearance of adambulacrals. Given the considerable width of the adambulacrals, small differences in attitude may make significant differences to perceived width. This feature must be considered unacceptable as a generic discriminator at least in the degree of widening. In the same key, Spencer (1930) distinguished a 3rd closely related genus, *Mastigactis* by its adambulacrals being of uniform width throughout the arm. Whether this uniformity is the result of the entire arm having been buried without any lateral rotation of the adambulacrals is not easy to determine without reference to the specimens and should remain an open question.

Recognising that a key seeks to limit the number of features by which to make easy recognition of taxa a search of discussion of the 2 genera following the key reveals very few comparative statements. Spencer (1930: 418) stated *Encrinaster* may be distinguished by comparatively long thin arms containing many segments and that marginal disc plates of *Encrinaster* bear long spines. The number of segments in each arm determines the length of the arm and the number increases with growth so this is a very growth related difference; measurements of all illustrated specimens of the 2 genera fail to show any clear cut differentiation. These linked and growth related features do separate the forms that Spencer (1930) figured in the work in which he erected the second genus. Similarly the long spines on the marginal plates in *E. grayae* are not evident in the type species or in most other species of the genus. Thus the features quoted by Spencer (1930) are parochial in their discriminatory application and are not suitable generic features on a broader scale. Thus we synonymise *Encrinaster* and *Euzonosoma*.

Encrinaster tischbeinianus (Roemer, 1863) (Figs 40-43)

Aspidosoma tischbeinianum Roemer, 1863: 144, pl. 23, fig. 1a, b (not pl. 25, fig. 11); Schöndorf, 1910: 23 and synonmy listed therin.
Encrinaster tischbeinianus (Roemer); Schuchert, 1914: 244.
Euzonosoma tischbeinianum (Roemer); Spencer, 1930: 404; Lehmann, 1957: 25, pl. 4, figs 1, 4-6.
Hexura weitzi Spencer, 1950a: 300, figs 4, 5 (not figs 1-3).

MATERIAL. South Africa. B4500-4502, B4505, B4506, B4510, B4511, B4548 from the Voorstehoek Formation at Hottentots Kloof. SAMK1018 from Riet River N of Ceres on Wupperthal road. S side of farm which is also called Groote Rivier in the neighbourhood, from Voorstehoek Formation. SAM11908 from Gamkapoort. SUG299 from De Doorns. Spencer's specimen (1950a, figs 4,5). B4555 from Boplaas Farm in the Waboomberg Formation. B4563 from Swaarmoed Pass, 2.1km from Great Swaarmoed Farm, near Ceres. RUGDNH2 from the Tra-Tra Formation.

DIAGNOSIS. Reaching large size (130mm arm length); with arms distally whip-like; disc with concave margins (of more than 11) large plates between arms; rest of disc of thin tiny tuberculate plates; 1st ambulacrals short and stubby; ambulacral groove wide across disc (apparently unable to close?); ambulacrals and adambulacrals as boot-shaped ossicles with toes pointing at each other; podial basins circular, similarly sized throughout arm; width of arm determined by width of ambulacrals or attitude of adambulacrals; madreporite ventral, adjacent to mouth frame, with strong ridge ornament.

DESCRIPTION. *Overall form.* Arms up to 130mm long (95mm max. in South African material), petaloid, widest at disc margin (up to 5mm), tapering strongly in distal part, distally whip-like. Disc pentastellate, with concave disc margins between arms, diameter 7-40mm, 0.5 or more of arm length, with margin of large irregularly polygonal plates sometimes extending a 2nd or 3rd row away from margin, remainder of surface a tuberculate apparently lightly mineralised integument, with larger tubercles close to mouth frame ventrally, especially in larger specimens.
Arm plating. Within the disc arms fixed into the plating, with adambulacrals and ambulacrals on

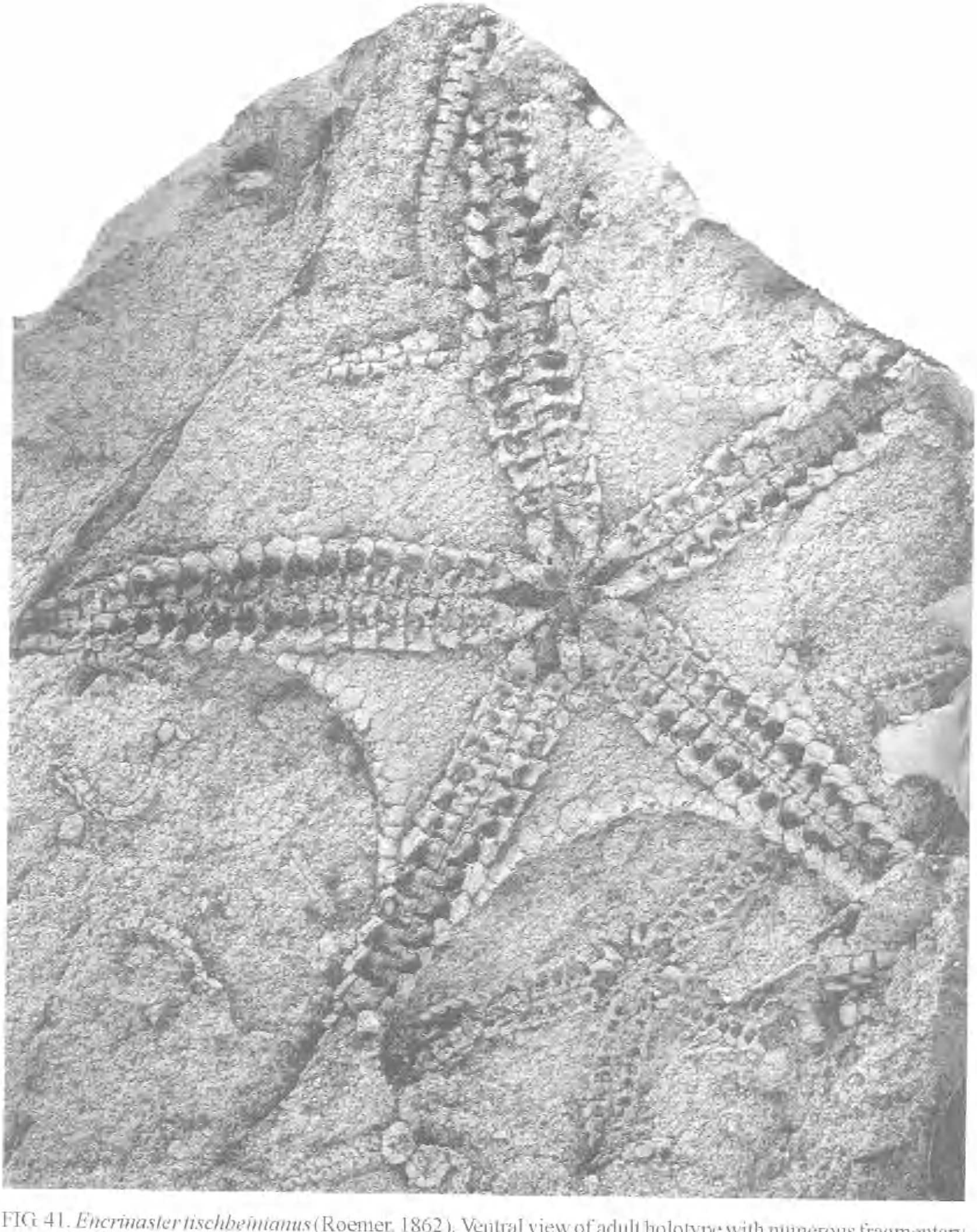


FIG. 41. *Encrinaster tischbeinianus* (Roemer, 1862). Ventral view of adult holotype with numerous fragmentary juveniles in both ventral and dorsal views, B4501 ×3.5.

same level suggesting ambulacral groove may be wide open and unable to be closed. Towards disc margin adambulacrals extending ventrally beyond ambulacrals and laterally enclosing a wide, deep ambulacral groove. Within disc, ambulacrals wide, with boot-shaped ridges well

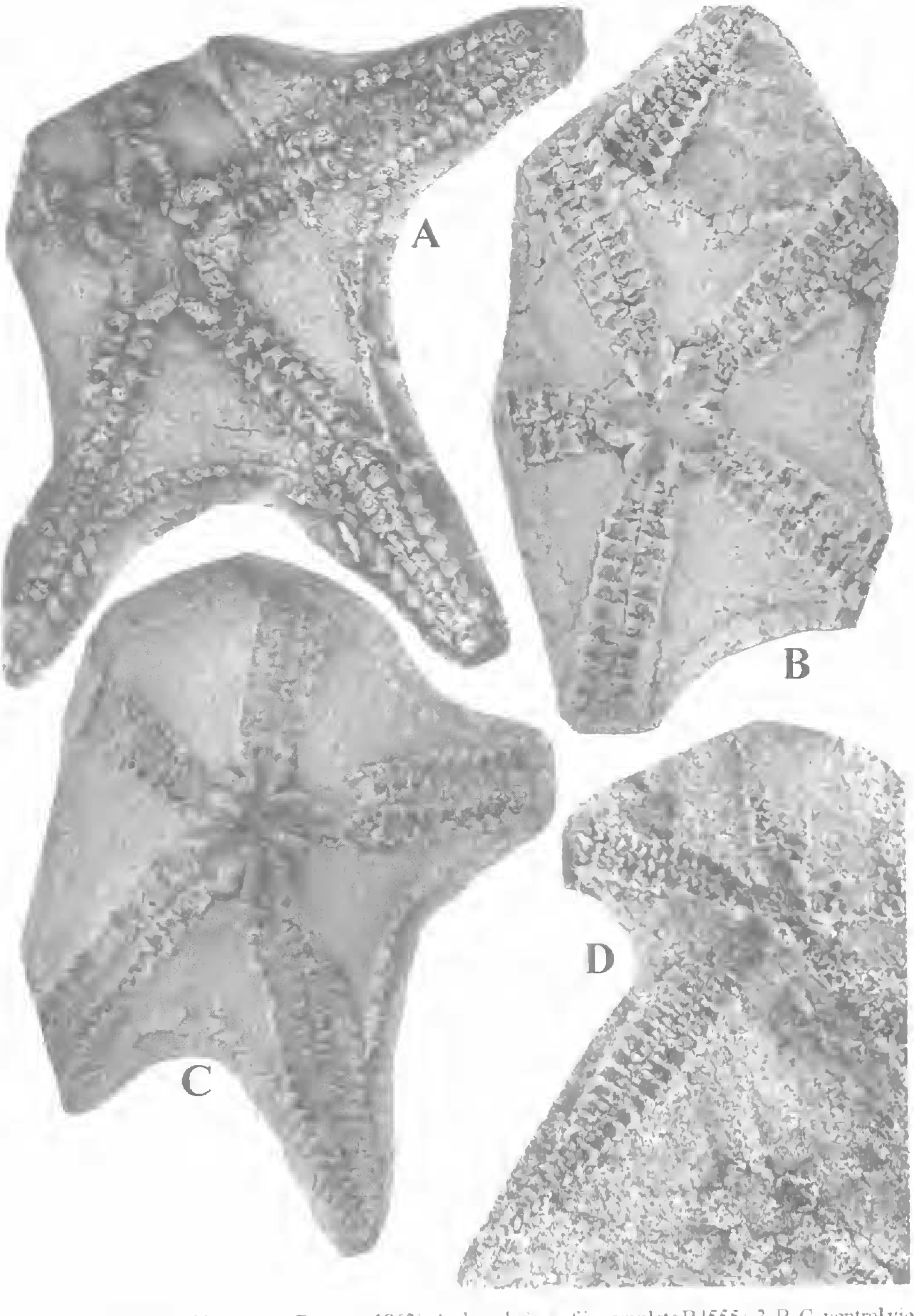
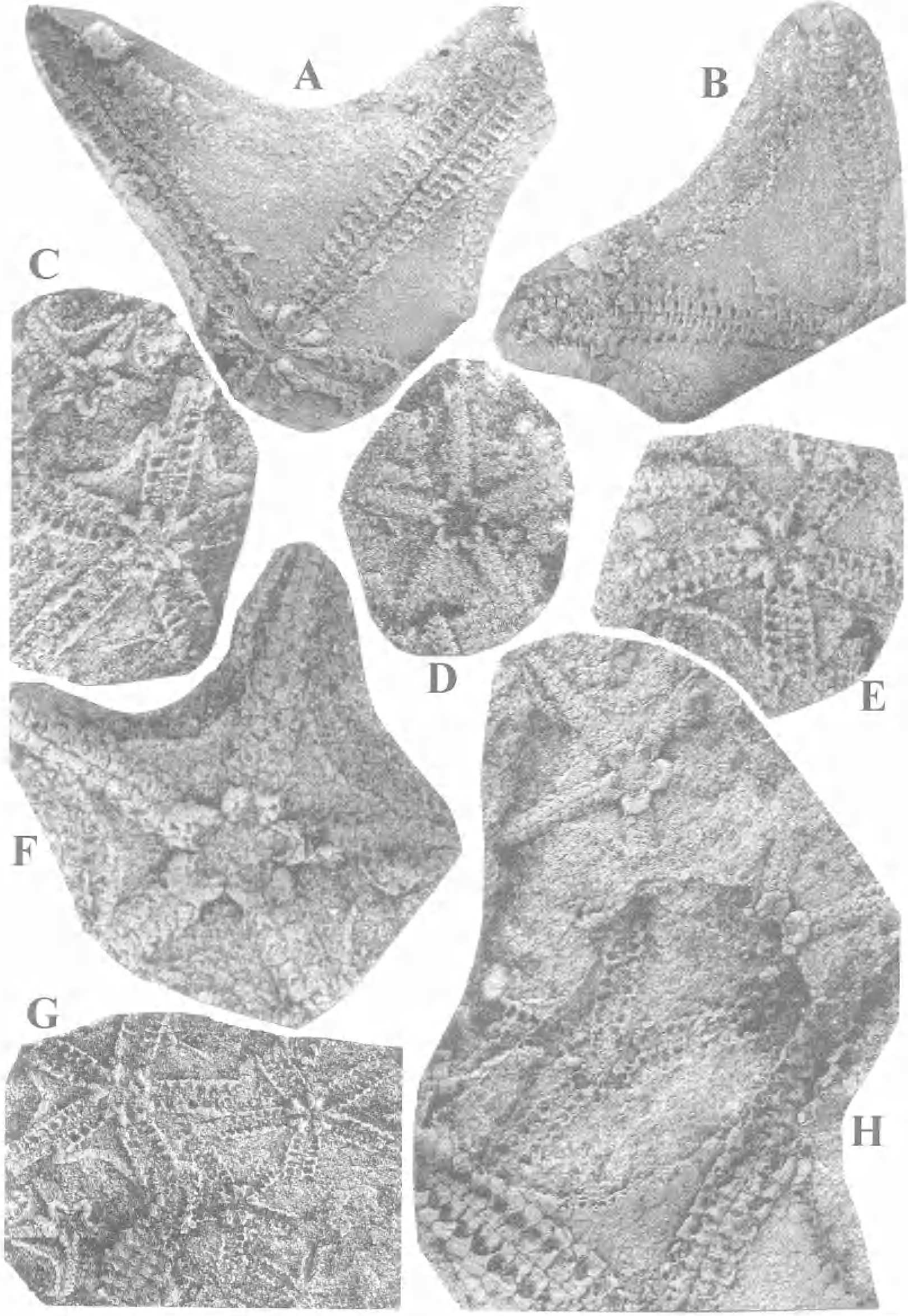


FIG 42. *Encrinaster tischbeinianus* (Roemer, 1862). A, dorsal view of incomplete B4555 ×3. B, C, ventral views of B4500 and SAM11908, respectively ×2. D, incomplete ventral view B4567 ×4.


A
B
C
D
E
F
G
H

away from the arm axis; near the disc margin, boot-shaped ridges closer to axis but arm of same width; distally, boot-shaped ridges contiguous along arm axis; ambulacrals narrowing abruptly to produce the whip-like termination.

Ambulacrals offset across arm axis; in dorsal view subquadrate, with narrow (becoming wider in larger specimens) but deep elliptical clefts between successive plates formed by concave proximal and distal faces for muscle insertion; proximal and distal margins raised as low ridges, with posterior rim extending abradially, with dorsal rim of concavity raised as a transverse ridge proximally, becoming less distinct distally as the interambulacral cleft becomes smaller and dorsal surface becomes subcylindrical (i.e., flat radially but curved transversely). Laterally this subcylindrical surface changes at a sharp line into a gently convex adradial side to the podial basin. Podial basin with floor having circular gap in the plates between ambulacrals and adambulacrals.

In ventral view, sutural junction between the 2 columns of ambulacrals obtusely zigzag (c. 160°). Proximal arm with thin, low, uniform, radial ridge along ambulacrals on each side of and close to (<0.5mm) arm axis; these ridges running to the suture along arm axis at about the disc margin. Abradial to this line each ambulacral with concavity facing arm axis and inclined on the side of the leg of the boot-shaped ridge. Prominently raised boot-shaped ridge with a strong constriction above the ankle and a long toe with distinct arch of the sole. Narrowest point (above the ankle) at midlength of podial basin on abradial side; small concavity (mentioned above) on adradial side. Abradial side concave, descending rapidly into the podial basin. Distally in the whip-like portion of the arm ambulacrals much narrower, lacking podial basins.

Adambulacrals. Shape and orientation of plates varying along column, with concommitant change in the ambulacral groove; ambulacrals 1 and 2 without associated adambulacrals. Adambulacrals proximally in dorsal view subtriangular, flat, in the same plane as the interradial surface, with articulation against ambulacrals a point separated from distal point by curved margin to aperture in floor of podial basin. Distinct groove parallel to axis along dorsal surface close to abradial margin, continuing along 6 plates beyond the disc margin, petering out as dorsal view of adambulacrals becomes progressively narrower. Adambulacrals changing from horizontal to almost vertical approaching disc margin, developing en echelon rather than linear arrangement; on 1 arm of the holotype 3 adambulacrals with bases of small spines attached to distal face (no other spines known). Adambulacrals almost vertical and subquadrate in lateral view just beyond the disc, distally becoming thinner, closer to the radial axis and enclosing arm more completely.

In ventral view, adambulacrals within disc as prominent L-shaped ridge with toe of base abutting against toe of boot-shaped ridge on ambulacral, with longer sections aligned and forming abradial margin of arm. Transverse ridge formed by toes of adjacent ambulacral and adambulacral almost knife-edged, of uniform height across both plates, giving very quadrate appearance to arms. Along abradial margins the continuity from plate to plate gives a sharp ridge along the whole arm to the disc margin. Gently sloping platform on adradial side of the L-shaped ridge descending into podial basins, formed by adradial face of adambulacral with ventral face directed laterally in this section of the arm. Approaching the disc margin podial basins smaller and deeper and adambulacrals arranged en echelon in column continuing so distally as adambulacrals become smaller but enclose the ambulacral groove more.

Mouthframe. 1st and 2nd ambulacrals conspicuous; tori and denticles rarely evident (dorsal margin of 1 torus (Fig. 42A) and a set of 3 denticles attached to a torus (Fig.41) are evident). 1st ambulacral with proximal ends vertical, bluntly pointed; groove for nerve ring extremely well impressed distal to where 1st Amb becomes higher and wider; groove for water ring wider and shallower, remaining on the mouthframe plates across the radial and interradial sutures so that the groove is evident as a full ring, with 2 pores in the groove on each 2nd ambulacral near the radial line of each arm. At the interradial junction between 1st ambulacra the water ring groove descends into the junction, creating a subcircular basin. 2nd ambulacral expanded only slightly distally, barely overlying any of 3rd ambulacral.

FIG. 43. *Encrinaster tischbeinianus* (Roemer, 1862). A-B, large incomplete individual in ventral and dorsal views, respectively, RUGDNH2 ×1.2. C,D, juvenile in ventral view, B4500 ×2. E, juvenile in ventral view, B4548 ×3. F, juvenile in dorsal view B4502 ×7. G, group of juveniles, B4500 ×2. H, group of juveniles, with adult at bottom, B4502 ×3.

In ventral view, proximal faces of adjacent 1st ambulacrals forming high concave recess to accommodate tori. 1st ambulacral extending well ventrally at edge of the mouth, descending steeply distally; suture between 1st and 2nd ambulacrals about halfway down this slope at widest point. 2nd Amb with small shallow podial basin on distal adradial corner and beginning of sharp longitudinal ridge of adambulacrals on distal abradial corner. Distal face of 2nd ambulacral near arm axis with small concave facet opposing the same on 3rd ambulacral, both for insertion of longitudinal muscles.

Madreporite. Interradially on ventral surface, just to the right of and contiguous with 2nd ambulacral, oval, outwardly convex, with irregular straight and curved grooves peripherally.

Disc. Dorsal surface a tessellated pavement of thin subquadrate to irregular plates each bearing a rounded tubercle, with margin of superior and inferior series of larger, thicker, differentiated plates without tubercles and with well defined sutural interplate boundaries. A few such plates are rarely seen in the second row from the margin.

REMARKS. Dorsally, available specimens show the plating of the mouthframe and arms without any suggestion of integument covering them; in life there must have been some sort of integument over the central mouth area and this probably extended out over the arms as well. It is probably of some unmineralised tissue that does not fossilise. How such an unmineralised integument related to the interradii is not clear; the obvious arrangement would see a 'skin' enclose the whole disc but then the reason for tubercles on plates becomes unclear if they are internal. If the integument covered only the mouth frame and arms the arrangement for its connection to the body between adambulacrals and interradial plates and its method of growth are obscure. Adambulacrals within disc have sutural junctions with the interradii on dorsal and ventral surfaces so the height of the body could not have been more than 1-2mm at this point as that is the height of the abradial wall of adambulacrals; this would leave a very flat body cavity within the disc and adds support to the possibility of an outer integument covering the entire body except for the ambulacral grooves and mouth.

This South African material conforms closely to the German *E. tischbeinianus* from the Lower Devonian Hunsrückschiefer in all features including relative disc size and shape, number of marginal disc plates, arm shape, relatively widely separated ambulacral column in each arm, and size and shape of the mouth frame. Considerably larger specimens are known from Germany but this disparity may be accounted for by the amount of collecting and by the German slates being a better matrix for yielding large whole specimens: in the coarser South African matrix the chances of obtaining large specimens is reduced. The finely tuberculate ornament on the disc is not evident on the German material but the slatey cleavage would be expected to obliterate such fine ornament. We consider all these discrepencies due to differences in preservation or intraspecific.

A number of very small specimens among the South African material give some information on growth of the species. In general the small specimens are virtually identical to the larger ones except that the mouth frame is not so robust, particularly in dorsal view; the arms appear to be of uniform width and the abradial aligned parts of the adambulacrals remain narrow and knife-edged throughout instead of thickening up and becoming en echelon arranged as in the larger specimens.

Marginura Haude, 1999

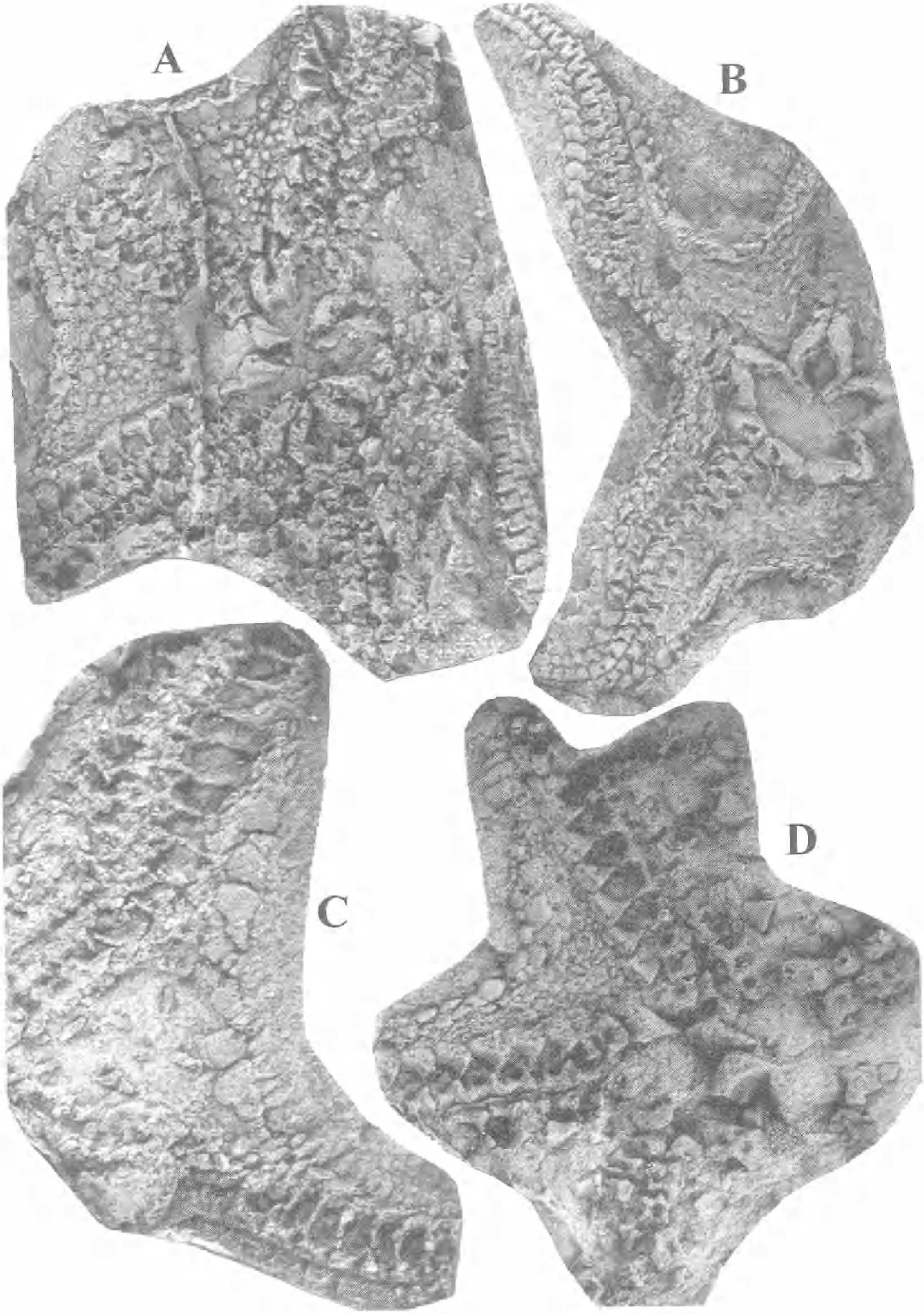
not *Marginaster* Perrier, 1881;
Marginaster Haude, 1995: 63.
Marginura Haude, 1999: 1.

TYPE SPECIES. *Encrinaster yachalensis* Ruedemann, 1916 from the Lower Devonian of western Argentina.

DIAGNOSIS (from Haude, 1995). Encrinasterinae with mosaic plated dorsal surface and interradii, concave margins to disc, concave outer margin of podial basin which has a round upper lamella.

REMARKS. This genus is only known from South America (Haude, 1995) and now South Africa.

FIG. 44. *Marginura hilleri* sp. nov. A, ventral view of disc including slightly disarticulated oral area B4566 ×3. B, dorsal view of incomplete specimen RO P84B ×3. C, ventral view of parts of 2 arms and an interradius with only marginal plating of latter remaining RO P84C ×5. D, ventral view of 2 arms, an interradius and the oral area with plates adjacent to mouth mainly disociated and possible madreporite at lower right RO E11 ×3.


A
B
C
D

Marginura hilleri sp. nov.
(Figs 44, 45)

ETYMOLOGY. For Dr Norton Hiller who contributed material for this study.

MATERIAL. HOLOTYPE: B4566 from Swaarmoed Pass, Ceres, 1.3 miles from Great Swaarmoed Farm. RO E11 from Damascus, Prince Albert at 33° 17'15"S; 21° 55'45"E. ROP84 from Swaarmoed Pass, Ceres at 33°21'30"S; 19°30'30"E.

DIAGNOSIS. Disc surface a mosaic of polygonal plates; disc plates larger and subquadrate near the margin, much smaller, less regular and bearing strong circular tubercles proximally. Adambulacrals with club-shaped abradial expansion, with L-shaped ridge running along proximal and then abradial margins. Ambulacral 2 extending dorsally over 3rd and 4th and with pointed distal extremity (not truncated). Abradial spatulate spines on arms apparently continuing along interradial disc margin.

DESCRIPTION. *Overall form.* Arms up to 40mm long, tapering distally, distally whip-like. Disc pentastellate, with concave disc margins between arms, with margin of large irregularly polygonal plates bearing marginal spines (2 per marginal), remainder of surface of small irregular tuberculate plates.

Arm plating. Within the disc arms fixed into the ventral plating. Distally adambulacrals extending further ventrally to enclose a narrowing but deeper ambulacral groove. [Within disc ambulacrals wide, with boot-shaped ridges well away from the arm axis; near the disc margin boot-shaped ridges closer to axis but arm of same width; distally boot-shaped ridges contiguous along arm axis; ambulacrals narrowing dramatically to produce the whip-like termination.]

Ambulacrals offset across arm axis, with straight intercolumn suture along arm axis, proximally much wider than long in dorsal view but in 2 distinct sections: 1, a subquadrate raised adradial section with 1-2 tubercles on a fine granular background ornament and 2, an abradial section down a distinct abradial slope (abradial section becoming narrower distally along arm and disappearing at beginning of whip-like section), with wide deep elliptical clefts between successive plates formed by concave proximal and distal faces for muscle insertion; proximally dorsal proximal and distal margins with fine low ridges.

In ventral view arm axis with straight sutural junction and distinct ambulacral channel between the 2 columns of ambulacrals; each ambulacral concave towards arm axis (i.e. back of leg of boot shape). Prominently raised boot-shaped ridge with short leg, strong constriction above the ankle and a long toe with distinct arch of the sole; with narrowest point (above the ankle) at midlength of podial basin, with concave abradial side descending rapidly into the podial basin. Ambulacrals much narrower distally in the whip-like portion of the arm, apparently lacking podial basins.

Adambulacrals. Shape and orientation of plates varying distally along column, shaped like the head of a large golf club (a 'wood') with transverse projection (the shaft of the golf club) abutting the toe of the ambulacral 'boot'; ambulacrals 1 and 2 without associated adambulacrals. Adambulacrals subquadrate in dorsal view, with articulation against ambulacrals at 2 points (anterior and posterior), with concave adradial margin in between combining with concave abradial margin of ambulacrals to define perforation through bottom of podial basin. Adambulacrals vertical throughout, forming lateral wall of arm.

In oral view, adambulacrals very thickened abradially, with continuity from plate to plate of expanded abradial parts producing sharp ridge along the whole arm being base of lateral wall, with gently sloping platform on adradial side descending into podial basins, with short wide spatulate lateral spines.

Mouthframe. 1st and 2nd ambulacrals fused into large unit as typically forms mouth frame throughout family but suture between them not evident on available material, dorsally overriding 3rd and 4th ambulacrals; tori and denticles not evident but a few acicular plates in oral region of one specimen (Fig. 44B) may be disaggregated denticles, with small narrow proximal ends; groove for nerve ring shallow and crossing paired 1st ambulacrals just proximal to groove for water vascular ring; groove for water ring wide, well-impressed, remaining on the mouthframe plates across the radial and interradial sutures (so that the groove is evident as a full ring), with 2 pores in the groove on each 2nd ambulacral near the radial line of each arm.

In ventral view, proximal faces of adjacent 1st ambulacrals forming relatively small concave recess to accommodate tori. 2nd Amb with small deep podial basin on distal adradial corner. Distal face of 2nd ambulacral near arm axis with small concave facet opposing the same on 3rd ambulacral, both for insertion of longitudinal muscles.

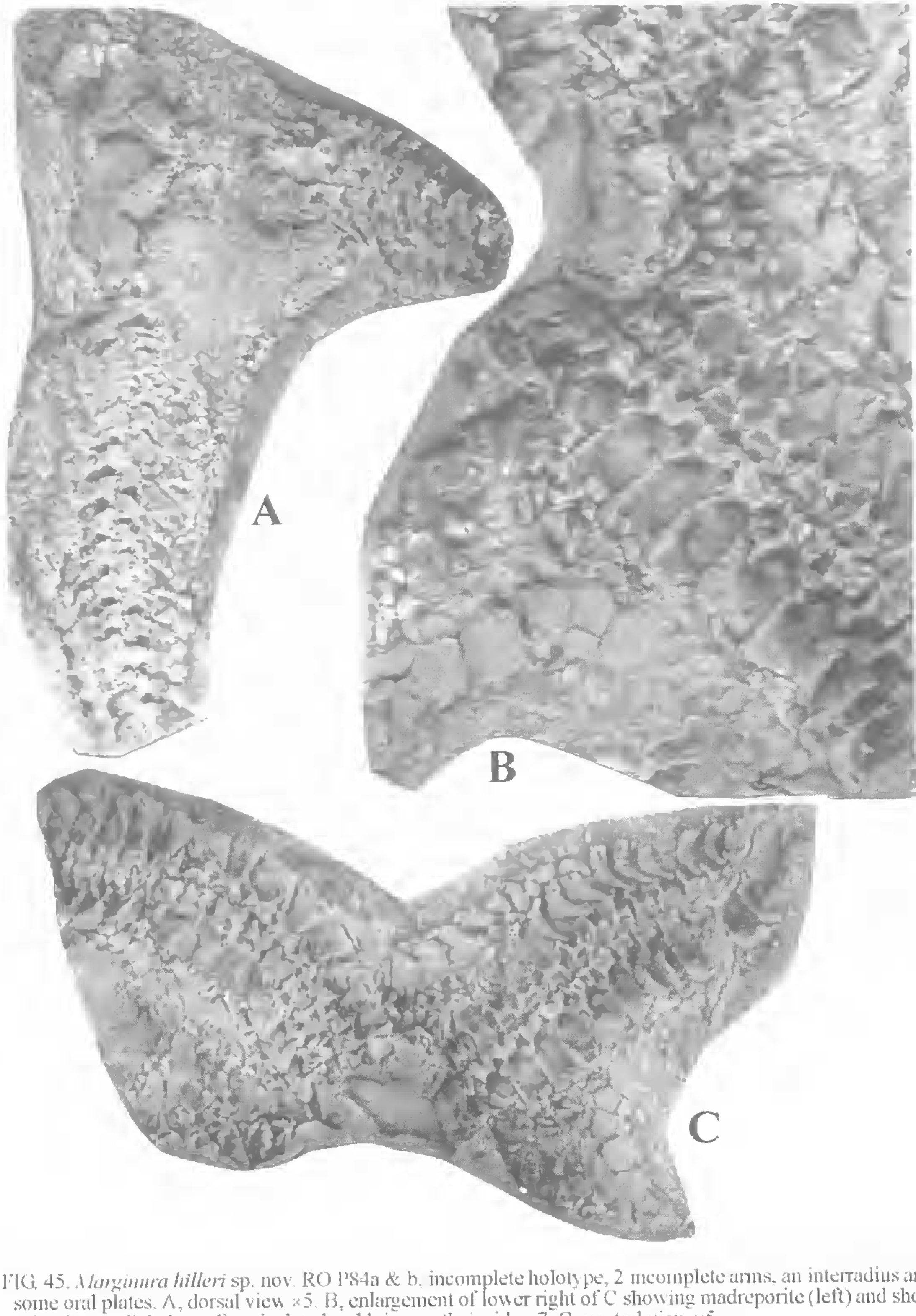


FIG. 45. *Marginura hilleri* sp. nov. RO P84a & b, incomplete holotype, 2 incomplete arms, an interradius and some oral plates. A, dorsal view ×5. B, enlargement of lower right of C showing madreporite (left) and short spiny interradial plates disarticulated and lying on their side ×7. C, ventral view ×5.

Madreporite. Interradially on ventral surface, suboval, with ornament of vermiform groove defined by sharp ridges.

REMARKS. This species is very close to the type and only congener, *M. yachalensis* but may be distinguished by its marginal spines, the pointed rather than truncated distal dorsal tips of the second ambulacrals, the course of the sharp ridge on the ventral side of the adambulacrals and the size of the tubercles or small spines on the ventral interradial disc plates, particularly proximally. The new species does not contradict any of the structural interpretation of Haude (1995).

Family PROTASTERIDAE Miller, 1889

Eugasterella Schuchert, 1914

TYPE SPECIES. *Eugasterella logani* (Hall, 1858) from the Middle Devonian Hamilton Group of New York.

DIAGNOSIS. Arms 5, long, slender, tapering distally, without dorsal arm plates or dorsal spines. Disc circular, inflated; dorsal surface of polygonal plates covered by finely granular integument. Madreporite ventral. Mouth frame large; 1st ambulacral long, narrow; 2nd ambulacral large, stout, with well-developed grooves, apophyses and pores dorsally for directing water vascular and nervous systems. Ambulacrals boot-shaped in ventral view; ambulacral groove slightly sinuous; dorsal surface with wide deep excavations for dorsal longitudinal muscles; podial basins large and well-defined. Adambulacrals roughly ear-shaped, narrow, wrapped around sides of ambulacrals, with large nodes for attachment to toe of boot on ambulacrals, with vertical spines.

REMARKS. This diagnosis follows that of Harper (1985) with emendation as inferred by Hotchkiss (1993) who diagnosed *Stratasler*, emphasising features of dorsal arm structure.

Eugasterella africana sp. nov.
(Figs 46-48)

Hexura weitzi Spencer, 1950a: fig. 3 [not figs 1,2,4-6].

ETYMOLOGY. From Africa.

MATERIAL. HOLOTYPE: B4561a (a,b, dorsal and ventral external moulds). PARATYPES: B4561b and c all from Klipfontein near Swaarmoed Pass, Ceres, B4569 from Hex Rivier Pass on Montagu Road 14km from N9 turnoff and RO123 from Matroosberg, Worcester(Hex River Pass) (33°30'S, 19° 48'E); all from the Voorstehoek formation. SAMK1014, 1015 from Verstehoek Formation at Riet Rivier (i.e. Gydo Formation, N of Ceres Division on Wupperthal Road; S side of farm which is also called Groot Rivier in the neighbourhood.

DIAGNOSIS. Arms slender, tapering gently throughout. Disc subrounded to subpentangular, inflated dorsally; dorsal surface of thin plates covered by a finely tuberculate integument, without spines. Short spines in a central marginal triangle on ventral interradii. Ambulacrals boot-shaped, with leg and foot of about same length. Adambulacrals with row of spatulate spines along ventral edge and 1-2 vertical spines. Madreporite circular with marginal aperture around half circumference.

DESCRIPTION. *Overall form*. 5-armed, disc radius 5-8mm, arm length up to 35mm. Arms slender, 2-3mm wide at disc margin, tapering distally throughout (no arm tip available). Disc circular to subpentagonal, gently inflated dorsally, with dorsal surface of small thin irregularly shaped plates covered by finely granular integument, without any spines on dorsal surface; ventral interradii triangular, with same finely granular integument as dorsal surface covering a lattice-like arrangement of plates increasing in aperture sizes towards margin of disc, with short stout spines in triangular zone involving entire disc margin and a third corner interradially about 1/3 disc radius away from margin.

Arm plating. Dorsal surface of arms circular in section, with many small thin irregular plates possibly elongate across arm axis and irregularly with small nodes. Ambulacrals offset along arm axis; in dorsal view subtrapezoidal, with wide deep excavations proximally and distally for longitudinal muscles, with prominent (decreasing in prominence distally) transverse ridges proximally and distally above deep cleft for muscle attachment, slightly sinuous axial line formed by concave adradial margin on each ambulacral into which a proximal and distal tip of successive ambulacrals from the opposite column project, the sinuosity decreasing distally; ventrally boot-shaped, with leg and foot of about equal length; ambulacral groove shallow, slightly sinuous as in dorsal aspect; podial basin round, deep, almost entirely on 1 ambulacral with corresponding adambulacral forming outer side to basin. Adambulacral abradial to and corresponding 1 to 1 to ambulacrals, planar, roughly ear-shaped, oriented vertically to form the lateral walls of the arm; in dorsal view only slightly abradially convex dorsal edge around short abradial edge of ambulacrals; in ventral

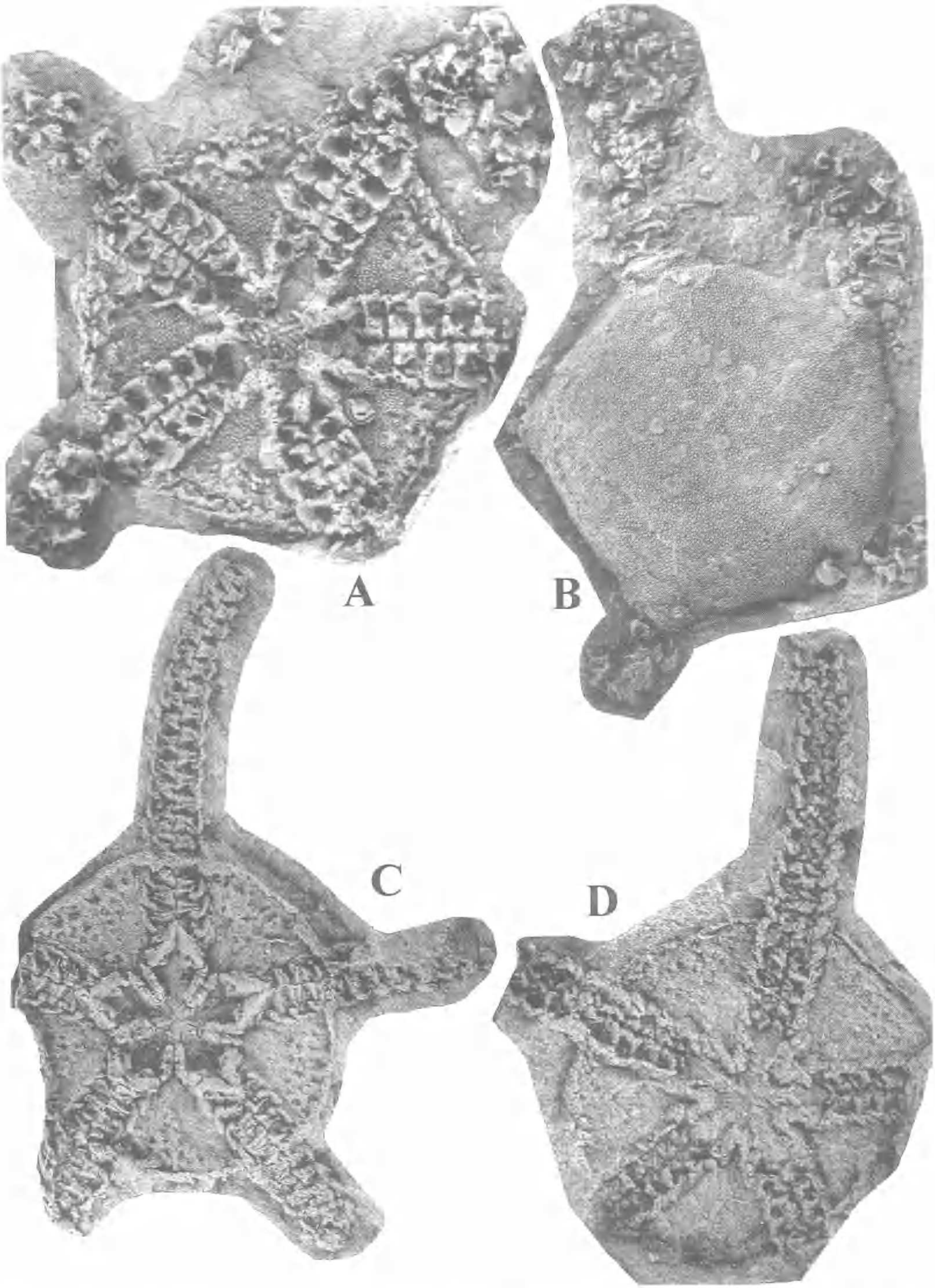


FIG. 46. *Eugasterella africana* sp. nov. A-B, ventral and dorsal views, respectively, of holotype B4561a & b ×4. C-D, dorsal and ventral views, repectively, of specimen with dorsal plating removed thus exposing proximal ambulacrals, tori and oral denticles (not evident with dorsal surface in place as in B) RO123a & b ×4.

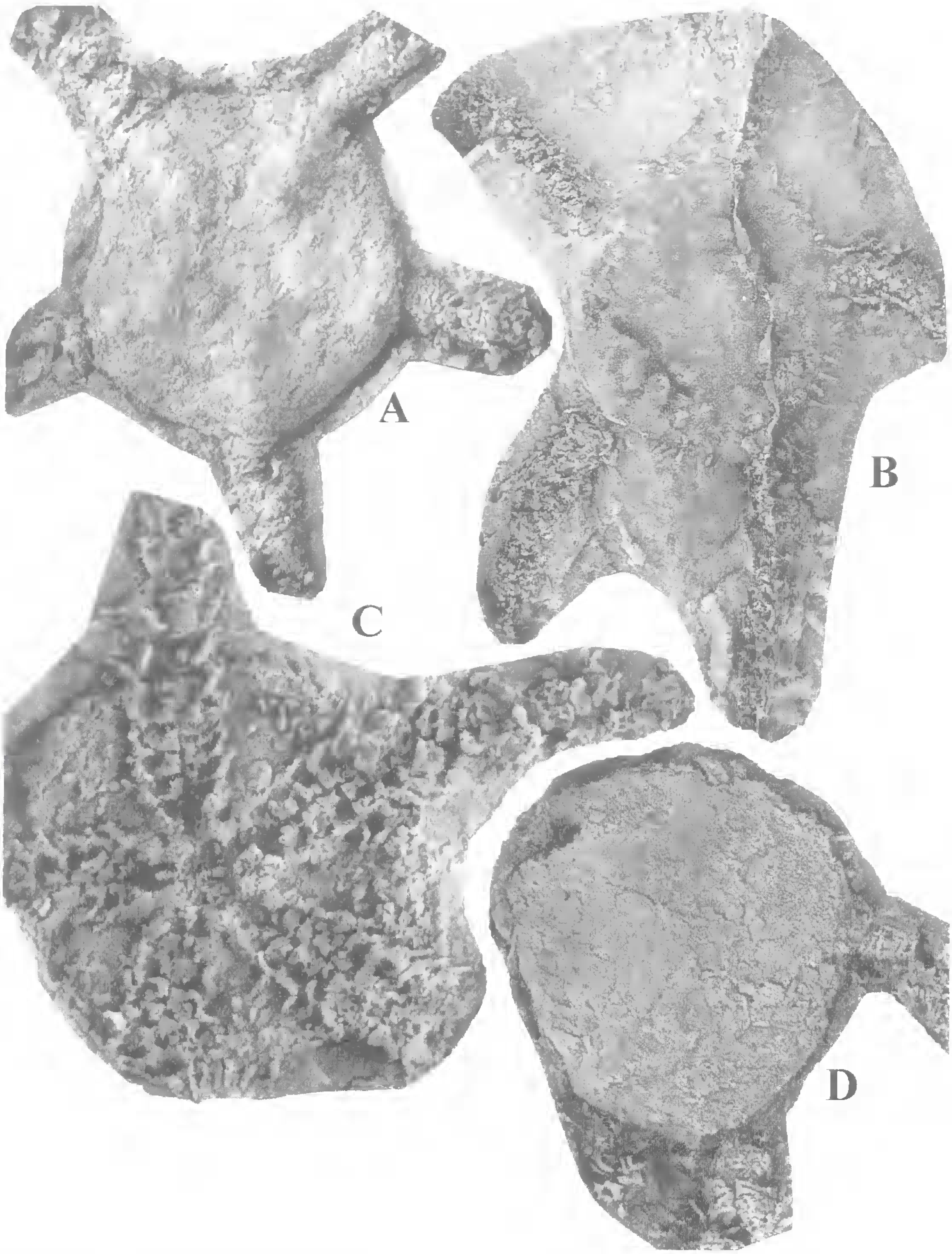


FIG. 47. *Eugasterella africana* sp. nov. A, dorsal view B4561E ×5. B, dorsal view with some longer spines in marginal interradial areas B4569 ×2.4. C, ventral view showing madreporite and marginal interradial spines B4561D, x6. D, dorsal view B4561C ×6.

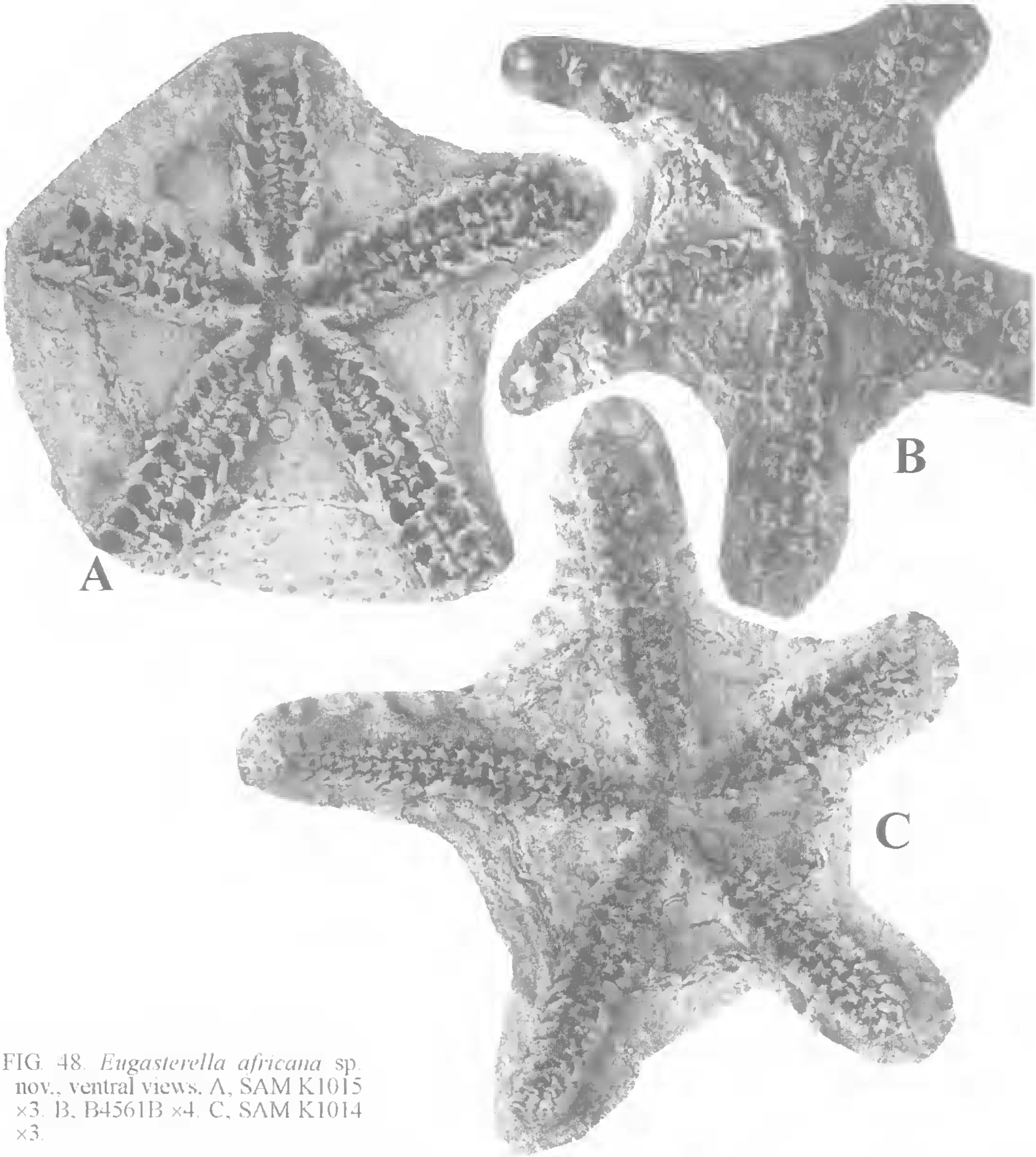


FIG. 48. *Eugasterella africana* sp. nov., ventral views. A, SAM K1015 ×3. B, B4561B ×4. C, SAM K1014 ×3.

view L-shaped, formed by strong lateral projection abutting toe of ambulacrals and narrow ventral edge in proximal-distal line, with line of 5 pits along narrow ventral edge each bearing short spatulate ventrally directed spine, with strong pointed spine directed distally arising from narrow platform formed by interruption to ventral edge towards distal end.

Madreporite. Ventral, to left in CD interradius, circular, convex, with broadly U-shaped slit-like opening close to and around 1/2 the circumference facing the D ray.

Mouth frame. In dorsal view occupying about 1/2 disc area; 1st ambulacrals in contiguous pairs interradially, elongate radially, straight, with transverse groove for nerve ring, pointed distal tip, with junction to 2nd ambulacral at 45° on outer distal bevelled face. Torus biconvex, fitting into concave proximal end of each pair of 1st ambulacrals, with horizontal row of 5 flat blunt spines projecting into mouth (central 3 wider than others); 2nd ambulacral large, forming strong V distally along arm, extending over next 2 or 3 ambulacrals, with groove for water vascular system on proximal side, extending along proximal 1/2 across distal ends of 1st ambulacrals, with 2 pits in groove on each plate (leading to podial basins of 2nd and 3rd ambulacrals. In ventral view 1st ambulacrals paired, forming narrow Vs, not contiguous as in dorsal view, straight, with concave proximal face, abutting 2nd ambulacrals on abaxial side of podial basin; 2nd ambulacrals with well-developed podial basin beginning column of basins of each arm; reduced adambulacral with 5 spatulate ventral spines not visible in dorsal view where covered by expanded 2nd ambulacral.

REMARKS. This species differs from the type, *E. logani* (Hall, 1858), from the Middle Devonian of New York in having marginal interradial spines on the disc, ambulacrals shorter and with deeper longer dorsal clefts between successive ambulacrals in each column and circular madreporite with slit-like aperture around most of its margin; it resembles more the only other assigned species, *E. devonicus* (Kesling, 1972) from the Middle Devonian of Ohio, in structure of the disc and in spinosity of adambulacrals although it appears to have a maximum of 2 vertical spines on each adambulacral as opposed to 4 in the North American species and may be further distinguished by the structure of the disc dorsally, which in *E. devonicus* was described by Kesling as having no discernible plates, thickly studded with small grains probably marking the position of papillae and bristly with short erect little spines.

Harper (1985, fig. 5) described and figured the dorsal surface of the disc of *E. logani* as composed of overlapping polygonal plates bearing raised biaxial ridges. The South African species suggests that these ridged plates are part of the ventral interradial plating (Figs 46C, D) which are evident in both dorsal and ventral moulds of specimens where the dorsal surface of the disc has been removed. We would interpret Harper's figure (1985, fig. 2C) as representing a specimen in which the dorsal surface of the disc was well-preserved only in the interradial triangle on the right of the specimen as viewed; some dorsal surface is evident in the other interradial areas except that at the upper left where the ventral or inner surface of the ventral plating is evident.

Strataster Kesling & Le Vasseur, 1971

TYPE SPECIES. *Strataster ohioensis* Kesling & Le Vasseur, 1971 from the Lower Carboniferous of Ohio; by original designation.

DIAGNOSIS. See Hotchkiss (1993:64).

Strataster ohioensis
Kesling & Le Vasseur, 1971
(Figs 49-53)

MATERIAL. South African material - B4509, B4512, B4513, B0195 -0197, B0276 and PRVT82 all from Boplaas Farm, N of Ceres in the Waboomberg Formation.

REMARKS. Some of these external moulds were coated with a thin layer of varnish after collection; this made them less absorbent and thus the latex casting has not been as successful as with other unvarnished material. The dorsal crest of each arm usually has a row of small air bubbles where the latex did not penetrate into the moulds of the carinal spines, but these spines are cast in a few places (Fig. 50C, 51B). The papillate dorsal disc integument is well preserved in several places draped over the strong mouth frame exactly as with Kesling and Le Vasseur's (1971) material; this indicates that the disc was distended with fluid or other soft tissue during life but had no solid material in it and no detritus in the gut. This is in contrast to *Eugasterella africana* where the disc has remained inflated indicating some solid disc filling such as sediment detritus or some structural integrity possibly conferred by the dorsal plating beneath the papillate surface.

This material agrees with the species described by Kesling & LeVasseur (1971) in every respect and as those authors gave an extremely detailed description there is nothing further to add. In particular, the upper arm plates and row of carinal spines, considered by Hotchkiss (1993), to be generic features occur in the South African material. The dorsal clefts between ambulacrals appear sharper in some of the North American specimens but in the South African material the small dorsal arm plates are preserved in most places and the varnish applied to the external moulds has in most cases diminished the height of the ridges adjacent to the dorsal clefts.

The South African occurrence extends the range to become Early Devonian to Early Carboniferous (Tournaisian) and the geographic extent to include Laurentia and Gondwanaland encompassing the Appalachian and Malvinokaffric

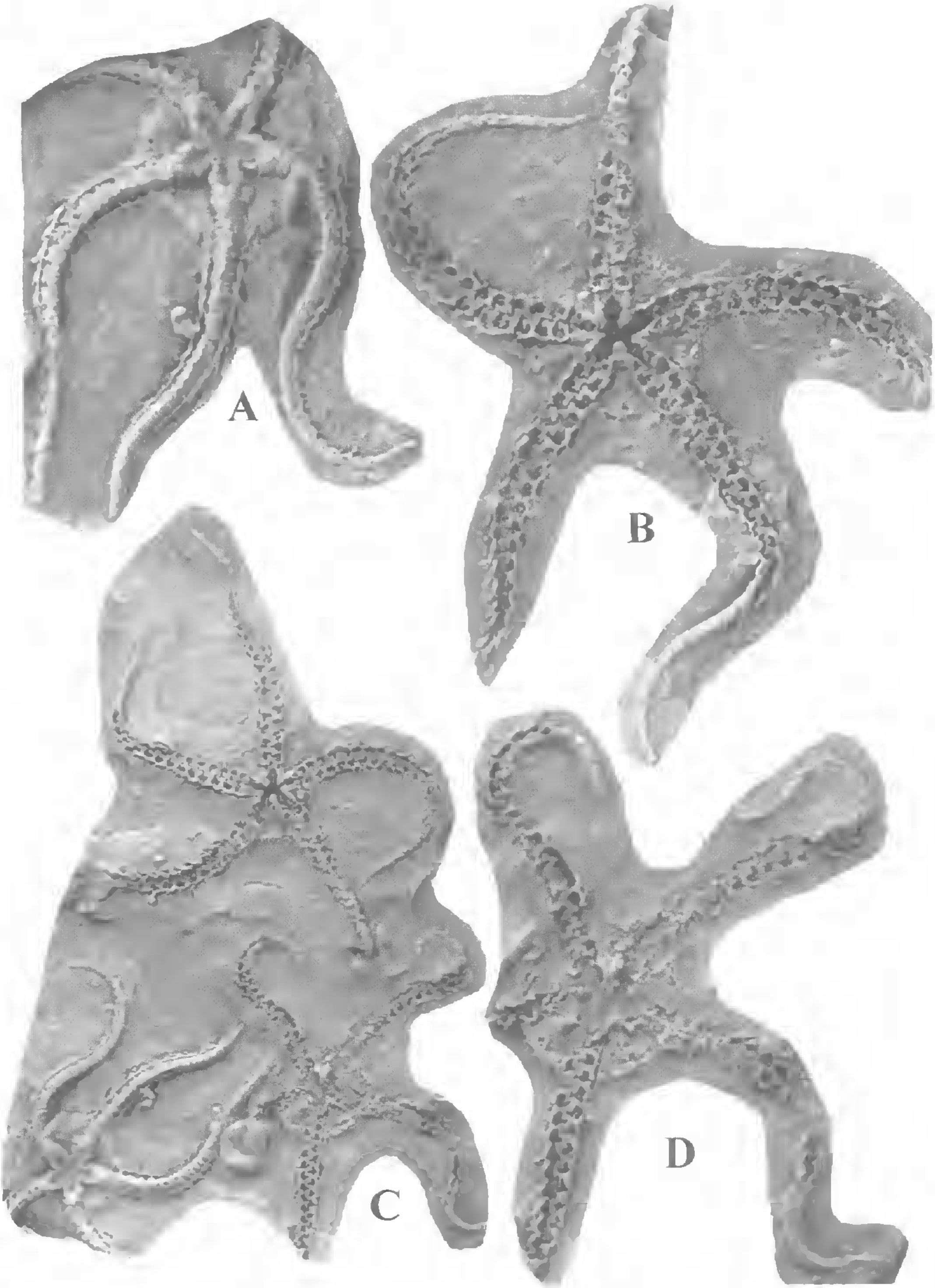


FIG. 49. *Stratister ohioensis* Kesling & Le Vasseur, 1971, group of 3 individuals B4513 (C) ×3. A, lower left specimen in dorsal view ×5. B, upper specimen in ventral view ×5. D, lower right specimen in ventral view ×5.

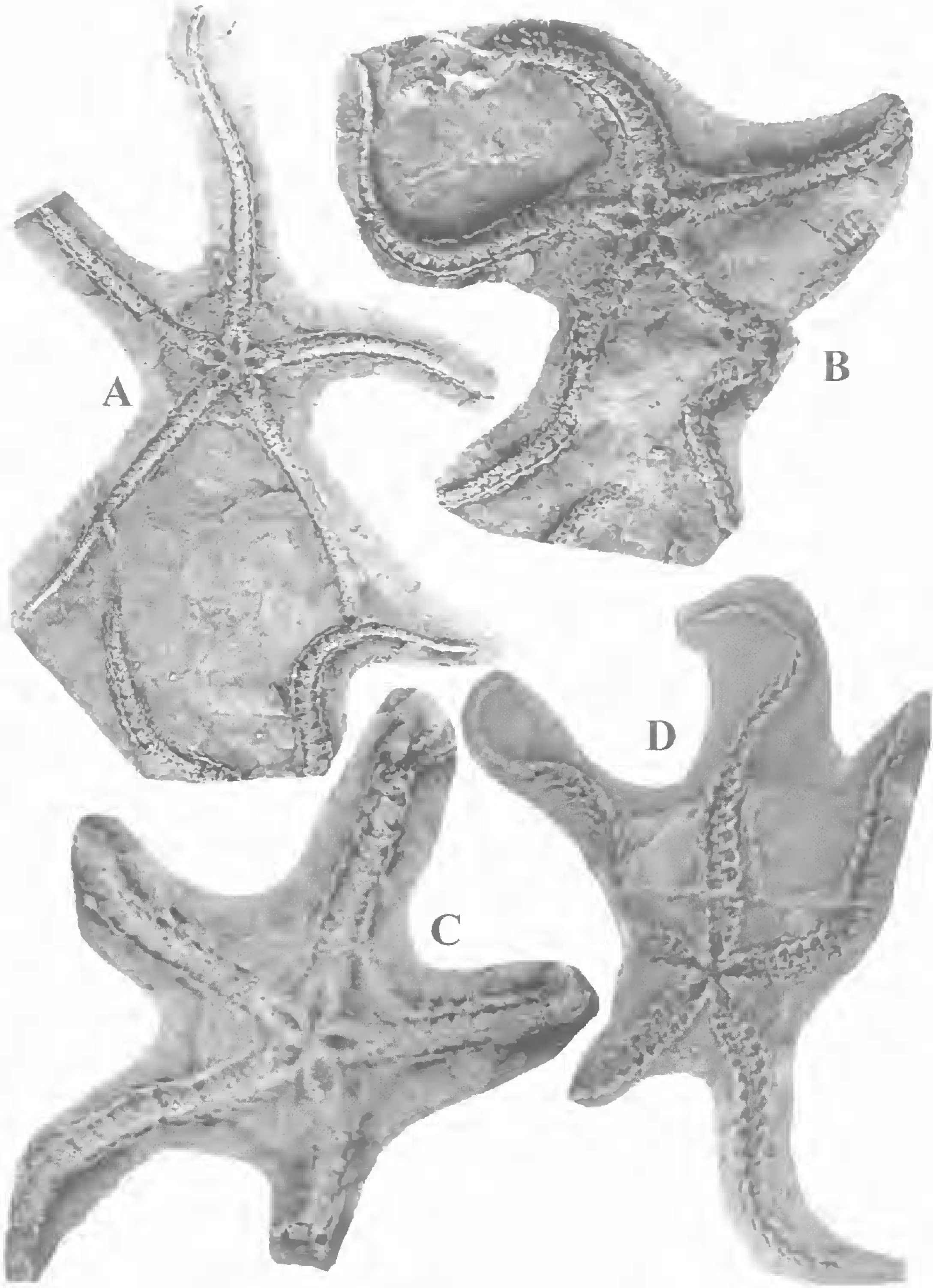


FIG. 50. *Strataster ohioensis* Kesling & Le Vasseur, 1971. A-B, dorsal views B4509A & B, ×4. C, dorsal view PRV T82A, ×4. D, ventral view showing madreporite B0276, ×4.

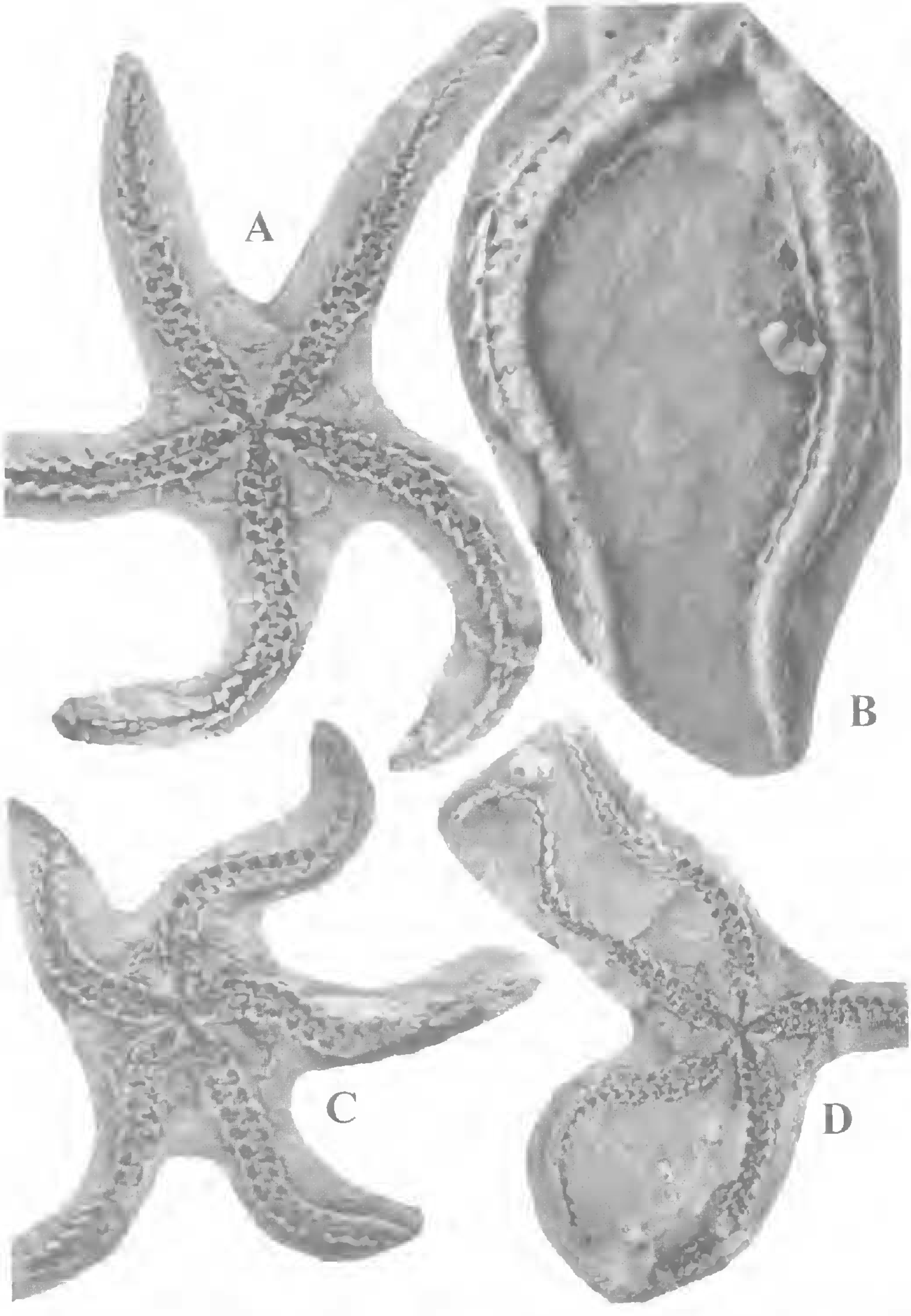


FIG. 51. *Strataster ohioensis* Kesling & Le Vasseur, 1971. A, ventral view PRV T82B, ×6. B, enlargement of 2 arms from Fig. 37A to show the median row of dorsal spines on each B4513, ×10. C, ventral view B0196, ×4. D, ventral view B0276, ×4.

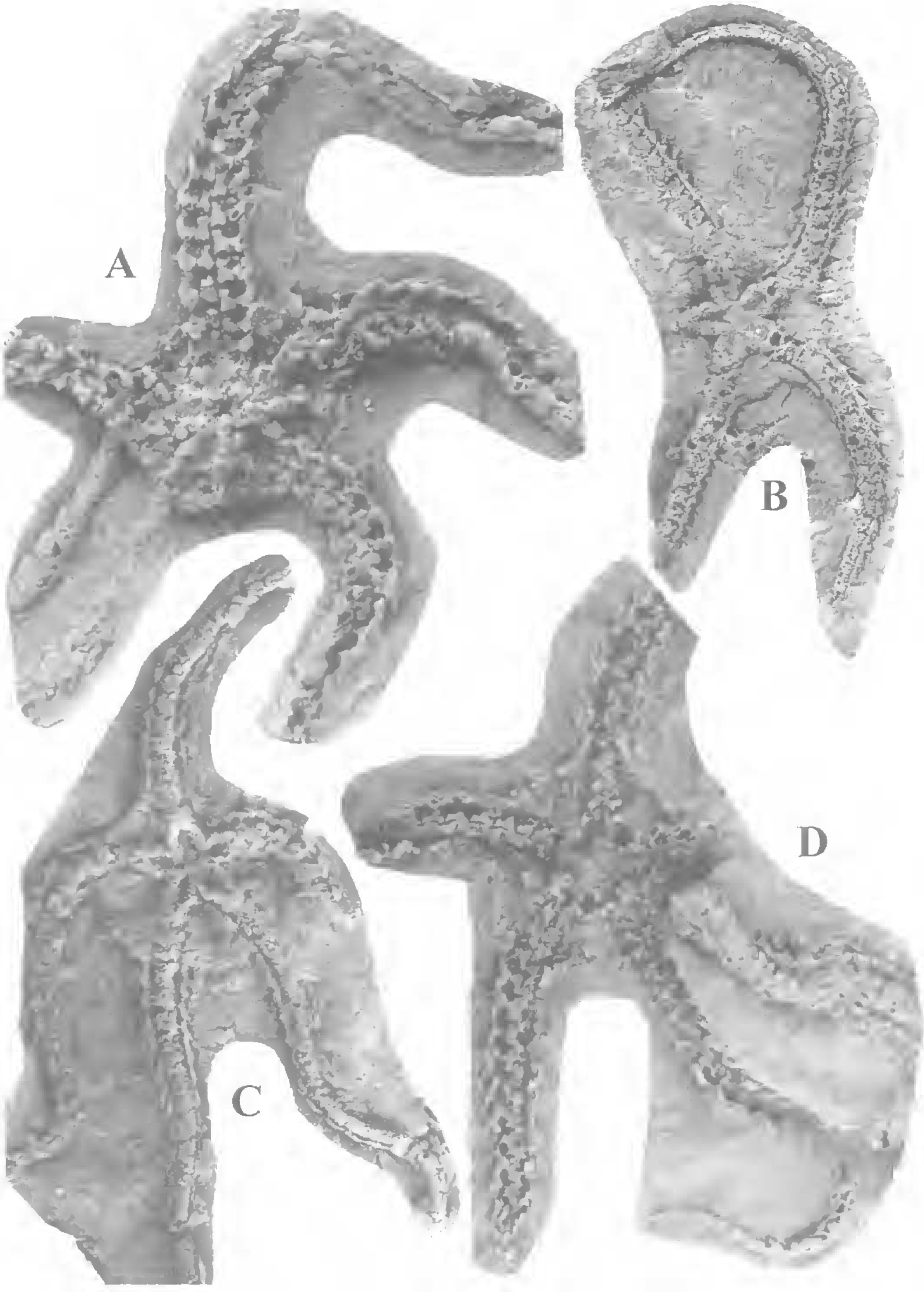


FIG. 52. *Strataster ohioensis* Kesling & Le Vasseur, 1971. A, ventral view B4509C, ×5. B, dorsal view B0197, ×4. C, dorsal view B4509D, ×5. D, ventral view with some of ventral disc plating removed so exposing dorsal plating from the interior of B4513, ×4.

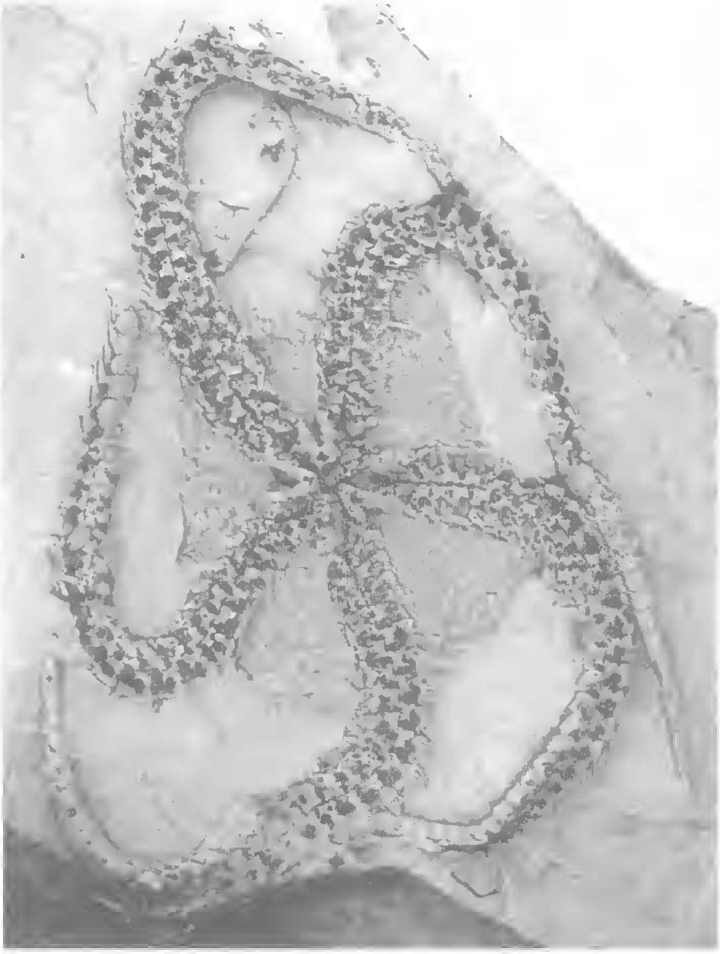


FIG. 53. *Strataster ohioensis* Kesling & Le Vasseur, 1971, ventral view of large individual B4512 ×3.

surface. Ambulacrals with short leg and longer foot to boot in ventral view. Adambulacrals with 6 or 7 curved, spatulate, ventral (or oral) spines, with 2 or 3 strong, straight, circular-sectioned lateral (vertical) spines. Madreporite large, circular, with slit-like aperture adjacent and parallel to margin for about 3/4 circumference.

DESCRIPTION. *Size and shape.* Average disc diameter among available specimens 15-20mm. Disc apparently circular; a few specimens suggest the disc may be extended slightly down each arm to give a substellate shape but this is probably due to postmortem movement. All available arms are preserved in curved position but are estimated to be 40-50mm long; arms widest at edge of disc (up to 4mm), tapering strongly distally to be <1mm wide over distal 10mm. The disc must have been flexible to some extent because angles between arms are not equal in any individual; while some of this may be due to postmortem forces it does indicate some ability for the arms to move towards and away from each other at least at the disc margin.

Ambulacrals. Alternating in 2 rows either side of a straight midline. Individual plates subrectangular, wider than long proximally, becoming longer than wide distally. Boot-shaped ridge prominent in ventral view, with a stout leg, projecting tips both back and forward up the leg, a distinct arch to the foot and a long toe abutting against the adambulacral. Podial basin deep, entirely on ambulacrals (with adambulacrals forming lateral wall of basin only). Distally (in whip-like section) no ambulacral groove, adambulacrals abut each other along the ventral midline. Dorsally 2 transverse ridges on each ambulacral; proximally these are close together near the midlength of the plate and converge slightly abaxially; between ambulacrals these high ridges are separated by wide deep V-shaped clefts for insertion of dorsal longitudinal muscles. Distally along the arm

Provinces of brachiopod palaeobiogeography (Boucot et al., 1969).

Some of the material referred to by Hotchkiss (1995) in his Appendix 1 at numbers 108-112 is included in this species.

Strataster stuckenbergi (Rilett, 1971) (Figs 54-56)

Taeniaster stuckenbergi Rilett, 1971: 32, figs 3-4.

MATERIAL. HOLOTYPE: NM Type 1550 on NM831 from near Ceres. OTHER MATERIAL: B4504 from the Waboomberg Formation at Theronsberg Pass, B4533, B4536 from the Voorstehoek Formation at Matroosberg.

DIAGNOSIS. Row of carinal spines on arms not extending onto disc or to arm tips. Disc integument dorsally and ventrally (interradii) with irregularly spaced spines on papillate

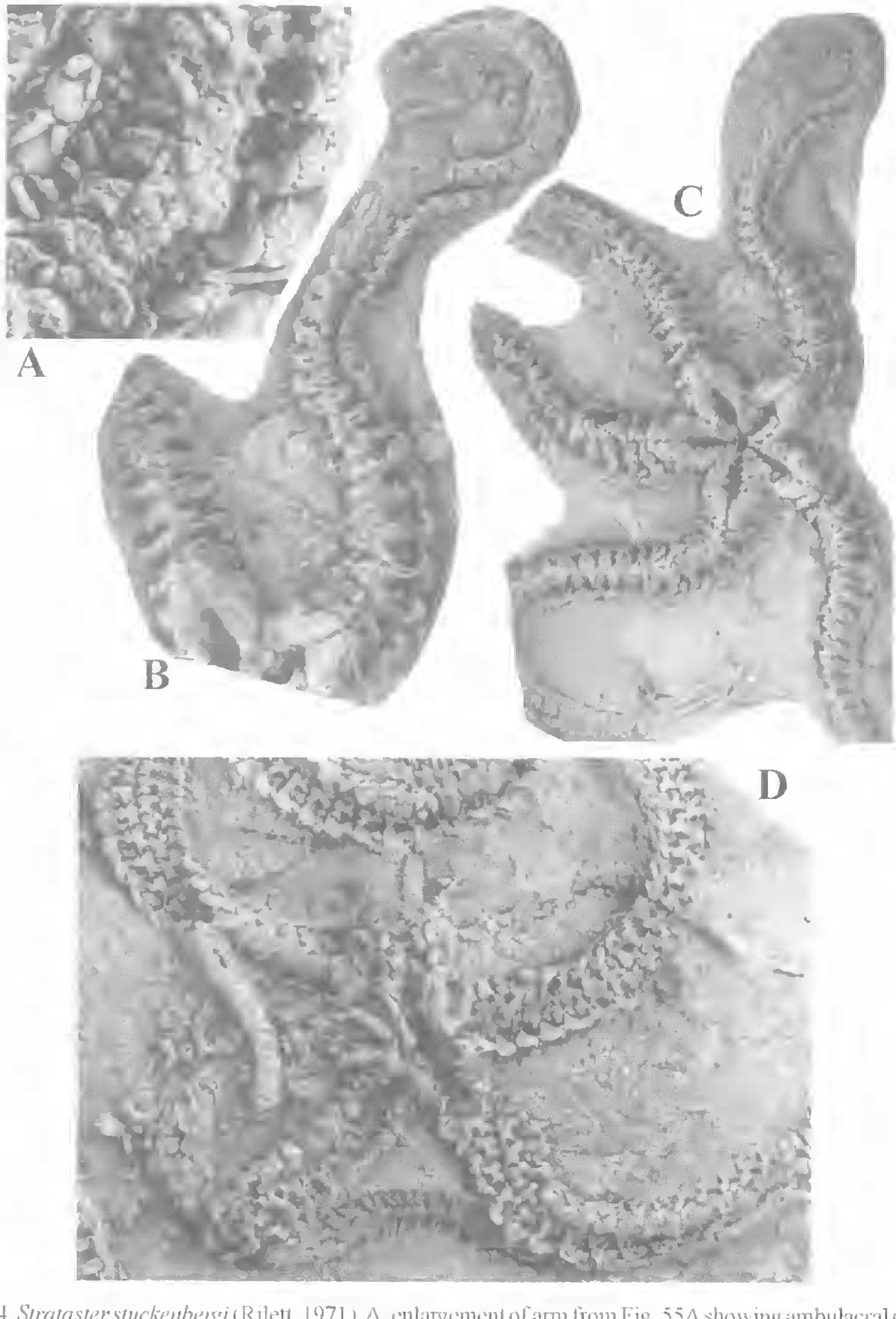


FIG. 54. *Strataster stuckenbergi* (Rilett, 1971). A, enlargement of arm from Fig. 55A showing ambulacral groove to right with 4 or 5 ventral spines on each Adambb on right of groove and larger lateral spines on outer side of Adambb on left of groove; also showing the row of median dorsal spines to left of ambulacrals and further left still a distal portion of another arm with lateral spines well exposed B4504 ×7. B-C, dorsal view showing deep clefts between ambulacrals and in enlargement (B) the row of mid dorsal spines and some interradial spines B4505 ×5. D, ventral view B4504 ×3.5.

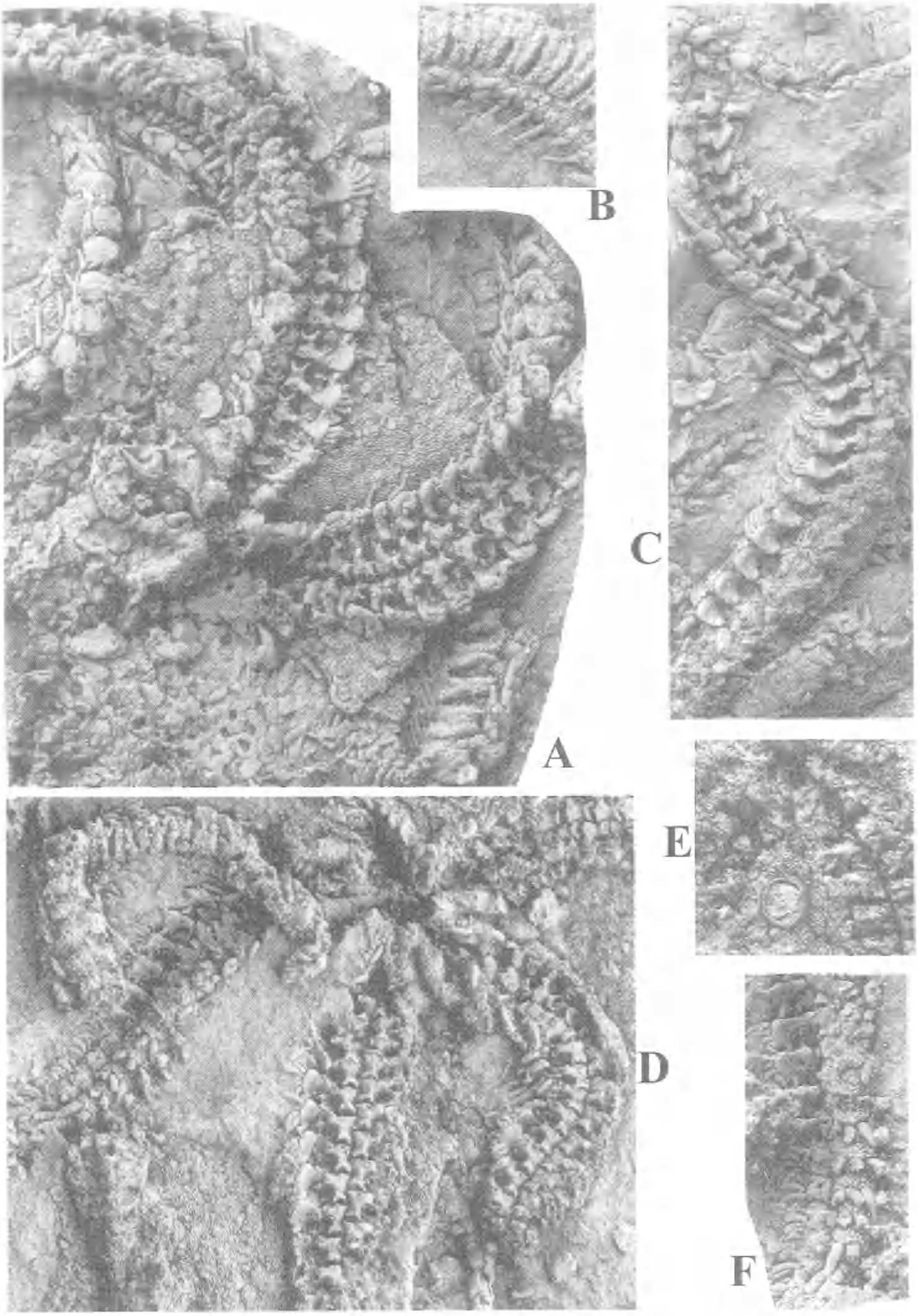


FIG. 55. *Stratasterstuckenbergi* (Rilett, 1971). A, ventral view showing madreporite, lateral and ventral spines on Adambb and plating in interradii in disc B4504 ×3.5. B, short section of arm showing long lateral spines on Adambb B4504 ×3.5. C, section of an arm showing spines on Adambb B4504 ×3.5. D, ventral view B4504 ×3.5. E, closeup of madreporite B4504 ×3.5. F, short section of an arm showing ventral spines on left and lateral spines on right B4504 ×3.5.

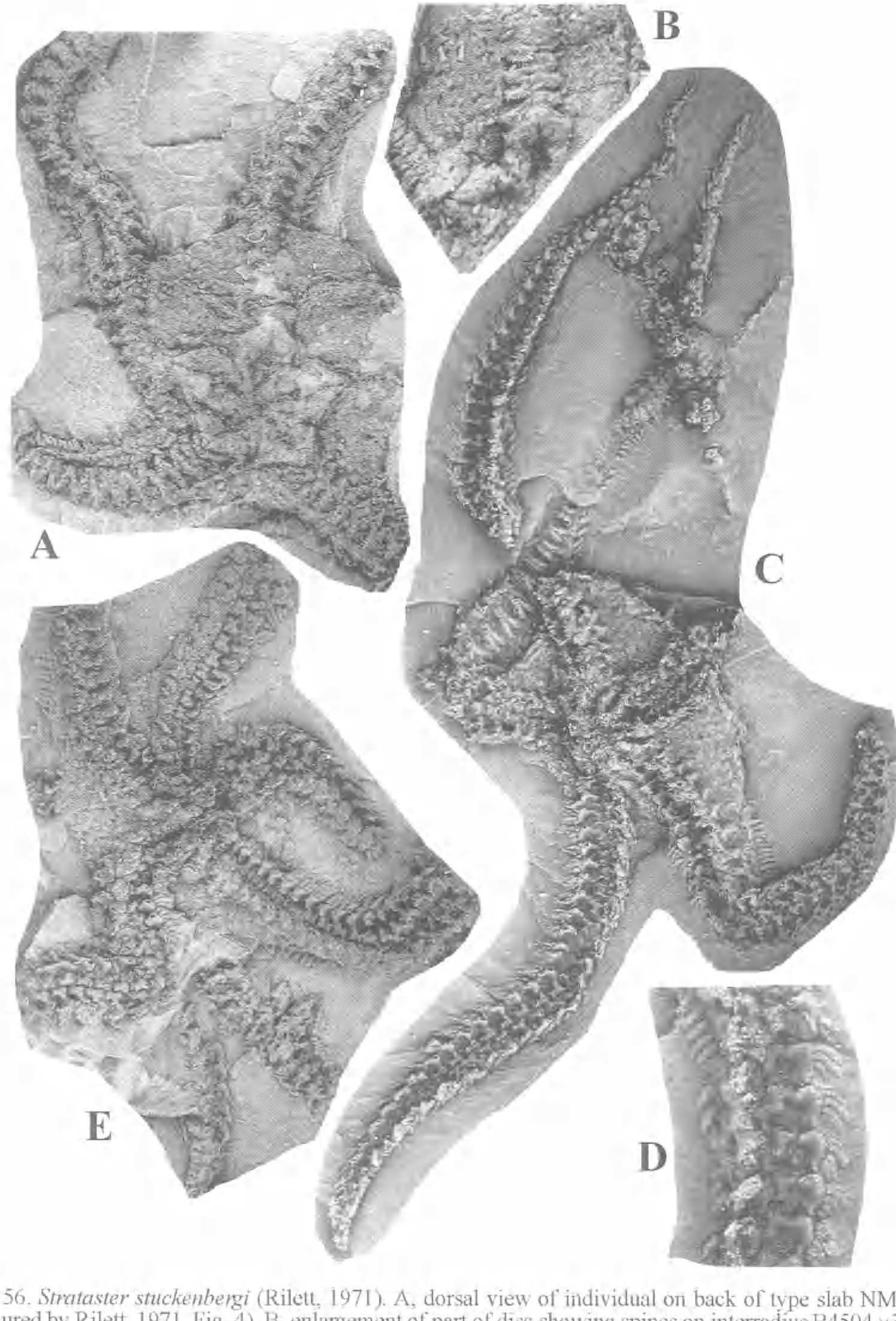


FIG. 56. *Strataster stuckenbergi* (Rilett, 1971). A, dorsal view of individual on back of type slab NM83 ×3 (figured by Rilett, 1971, Fig. 4). B, enlargement of part of disc showing spines on interradius B4504 ×3.4. C, ventral view of holotype showing the medial dorsal spine rows in several places NM type 1550 ×2.5. D, enlargement of upper arm in C in ventral view showing Adambb on both sides with ventral spines and at left the dorsal medial spine row ×5. E, ventral view of individual on back of NM831 ×2.5.

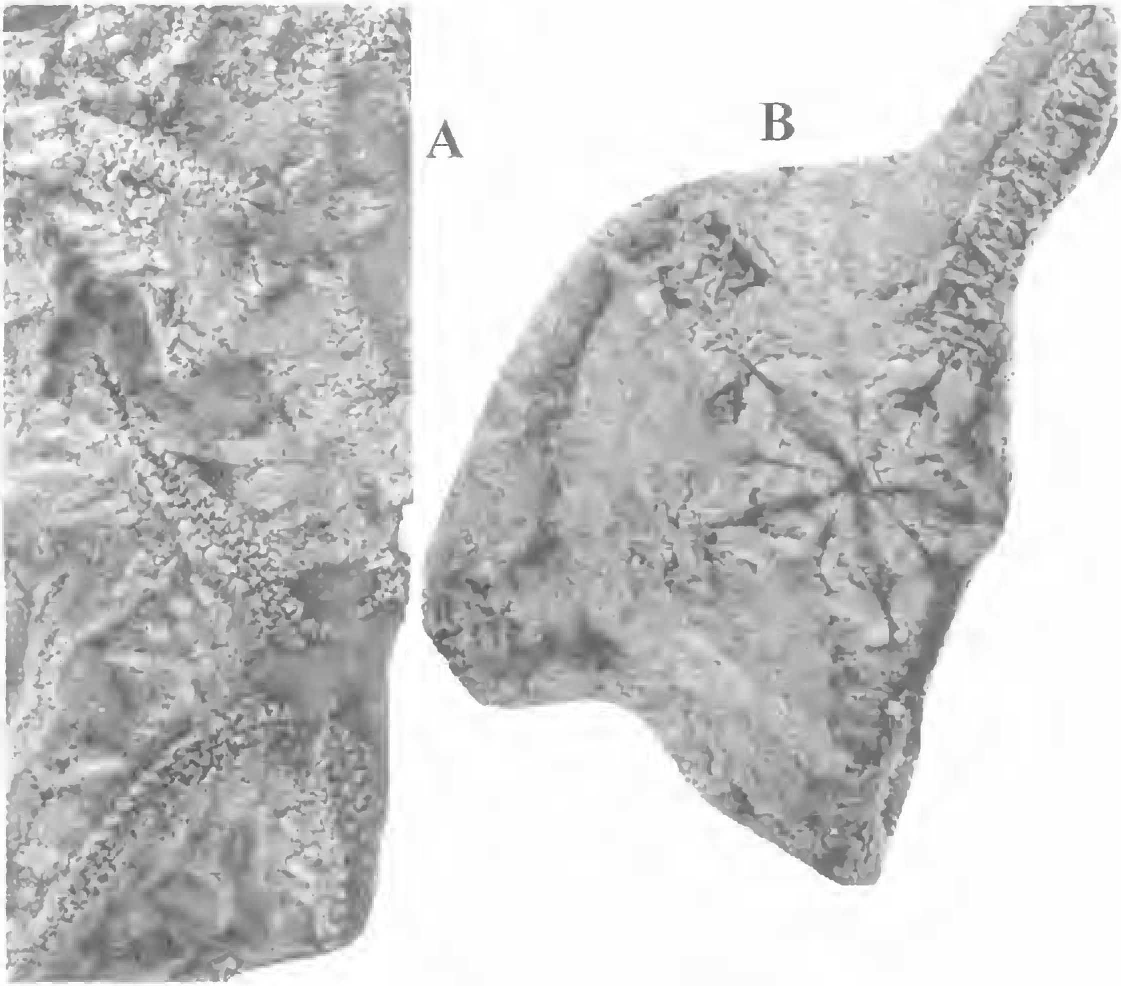


FIG. 57. *Stratastersp*. A, dorsal view (upper) of disc with arms broken off at disc margin and ventral view (lower) of individual with disc not preserved SAM13475 ×3. B, dorsal view of disc and proximal arms with tori in place and suggestion of medial dorsal spine row on arm at 8 o'clock PRV 3231 ×5

these ridges are parallel and further apart being near the proximal and distal edges of ambulacrals: still further distally (where ambulacrals subquadrate) the ridges not raised so, apart from the external integument, ambulacrals are then smooth, transversely convex and abut each other closely with only a narrow V-shaped cleft between plates. Junction of the 2 columns of ambulacrals is straight and capped by a line of prominent rounded dorsal spines on the free arm as far as the whip-like distal portion. Distally on the arms are papillae: skin a smooth tessellated pavement of small plates not extending over the entire adambulacral.

Adambulacrals (or laterals). One column of adambulacrals on each side of arms adjacent to ambulacrals. Each adambulacral gently convex (vertically), enclosing the arm laterally. Near its midheight is an adradial projection abutting the toe of the boot-shaped ridge on the ambulacral. Adradial margin of adambulacrals abutting ambulacrals along the outer edge of the floor of the podial basin. A shallow groove along the ventral edge, with 6 small pores at each of which is attached a curved (ventrally and distally) flattened spatulate spine: abradially on the distal margin (above the spatulate spines but in the same line as their groove) a pair of strong round tapering spines directed distally. Distally all spines are shorter, more slender, and progressively fewer in number. Abradially they form a distinctive lateral column of plates closing off the abradial sides of the deep clefts between ambulacrals. Their outer or abradial margins are set en echelon with a large part of the distal face free and bearing the 2-3 distally directed circular-sectioned spines.

Madreporite. Interradial, ventral, smooth, gently convex, with a U-shaped aperture close to the plate margin on 3 sides and with the inside of the U slightly elevated. Within the interradius it is closer to the ambulacrum at the base of the U. Integument of the disc extends over the madreporite at least in the area at the top of the U.

Disc. External integument highly flexible, probably collagenous skin, covered with closely spaced papillae and widely distributed short circular or oval (in section) spines which are mostly broken off and represented by their smooth bases. Skin compressed down from the aboral side into the depressions among the mouthframe, extending over the entire dorsal disc, over the entire ventral interradii including the mouth frame but excepting the ambulacral grooves and mouth, also covering arms dorsally and laterally. Where the outer integument is not preserved, a mosaic of irregularly shaped flat plates is exposed. These have numerous projections which overlap, leaving some gaps; outer integument where preserved, with irregular depressions corresponding in size and probably position to these gaps and which have central spines. There is no differentiation of a marginal rim to the disc among these underlying plates. These plates are not joined by sutures but probably provided any structural rigidity in the disc.

Mouthframe. Large star-shaped, occupying about 1/2 disc diameter and formed mostly by modified 1st and 2nd ambulacrals. Although the aboral view in each available specimen is obscured by the outer integument, one specimen (Fig. 55A) shows 3 denticles in place on a torus; the denticles are best exhibited in a few oral views where 10 or more denticles are evident in a bundle. The 1st ambulacrals [MAP of most authors] are modified into radially elongate form, arranged in pairs interradially [1 from each arm], crossed transversely by well impressed groove for the nerve ring, and sutured distally in an oblique suture to the 2nd Amb (1st Amb of most authors). The groove for the water vascular ring, which runs around the mouthframe, does so across the 1st-2nd ambul- acral sutures as in other protasterids. In dorsal view 2nd ambulacrals are greatly elongate distally and extend over the top of at least 3rd and 4th ambulacrals. In ventral view 2nd ambulacral has rudimentary podial basin but also has adambulacral of 2nd and 3rd ambulacrals along its adradial margin. Face of 2nd ambulacral articulating with 3rd ambulacral is very high and concave. Adambulacrals on the adradial side of the enlarged 2nd ambulacral is clear in 2 specimens right into the vertical face of 1st ambulacrals at the edge of the mouth. There is the appearance that the adambulacral column moves from abradial to adradial relative to the ambulacral column but we think it more likely that they move further ventrally as well so making the change of orientation less dramatic. Adambulacrals adjacent to 1st and 2nd ambulacrals retain their full complement of ventral spines.

REMARKS. This species would fit into *Taeniaster* among genera available in Spencer & Wright (1966) but Hotchkiss (1970) and Kesling & Le Vasseur (1971) discussed that genus and relatives at length and separated *Strataster* on the basis of the line of carinal spines on upper arm plates among other features. It is separated from *S. ohioensis* by the shape of the madreporite, length of ambulacrals along arm axis and numerous spines on disc dorsally.

Strataster sp.
(Fig. 57)

MATERIAL. SAM13476 and PRV3231 from the Verstehoek Formation on hill on S side of farm Riet Rivier (Grootrivier) at N end of Ceres Division on Wupperthal Road.

REMARKS. This material is referred to *Strataster* based on the bases of middorsal spines (Fig. 57B, arm at 8 o'clock), the very strong dorsal transverse ridges on ambulacrals, shape of the boot-shaped ridges in ventral view and structure of the mouth frame. However, the lack of detail of dorsal integument which is apparently a tessellated pavement of irregular plates giving a smooth surface, no complete arm and no ventral view of the mouth frame prevent assignment to a known species. We prefer to retain these specimens in open nomenclature at present.

Ophiuroid arms indet. B
(Fig. 58B, C)

MATERIAL. B4546a-e from the Voorstehoek Formation (C2S2) at dieVlakte.

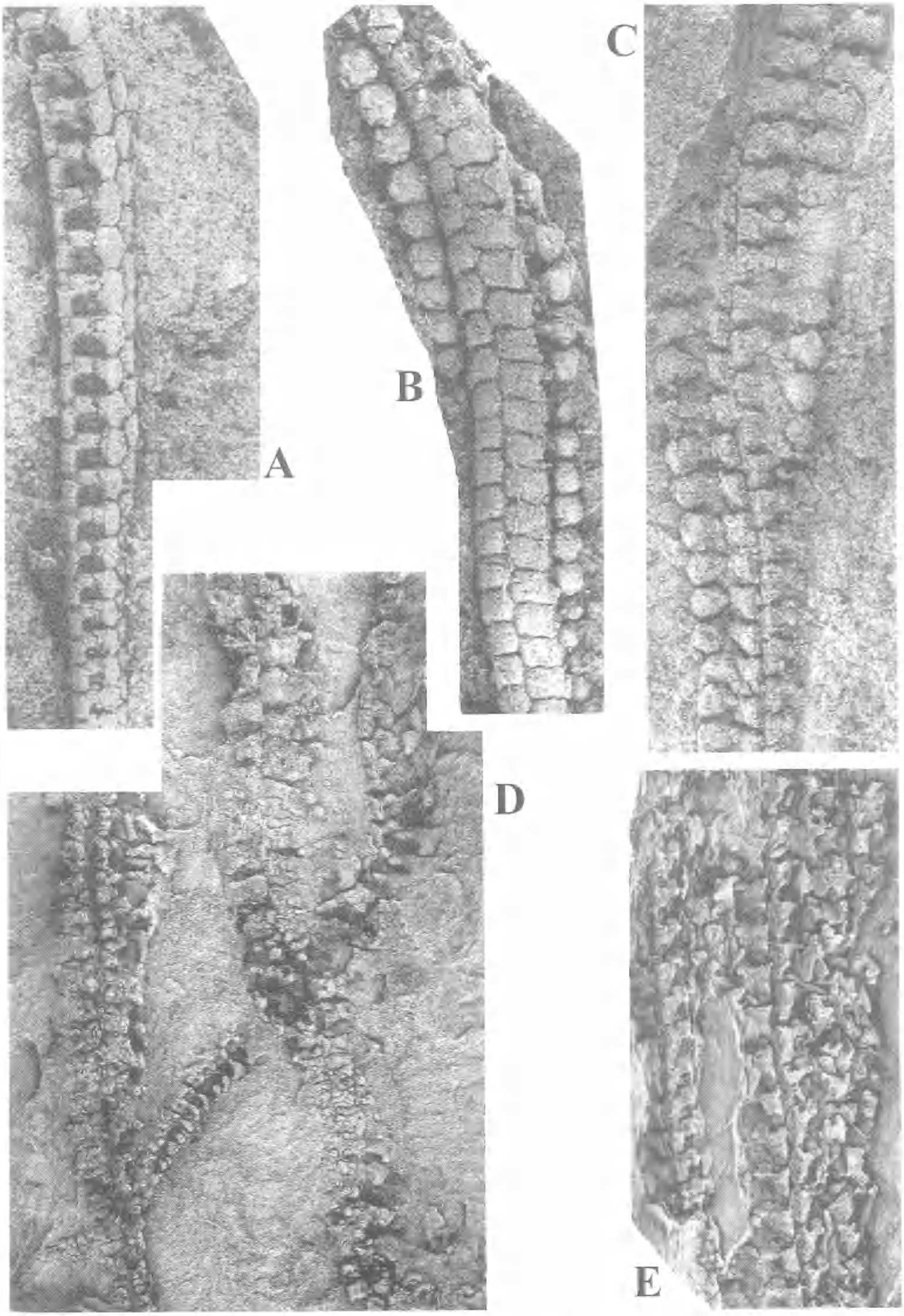


FIG. 58. A, Ophiuroid arm indet A. SAM K625 ×5. B-C, Ophiuroid arm indet B, dorsal (B) and ventral (C) views B4546 ×2. D-E, Ophiuroid arms indet C in ventral view B4560 and RO 745 ×2.

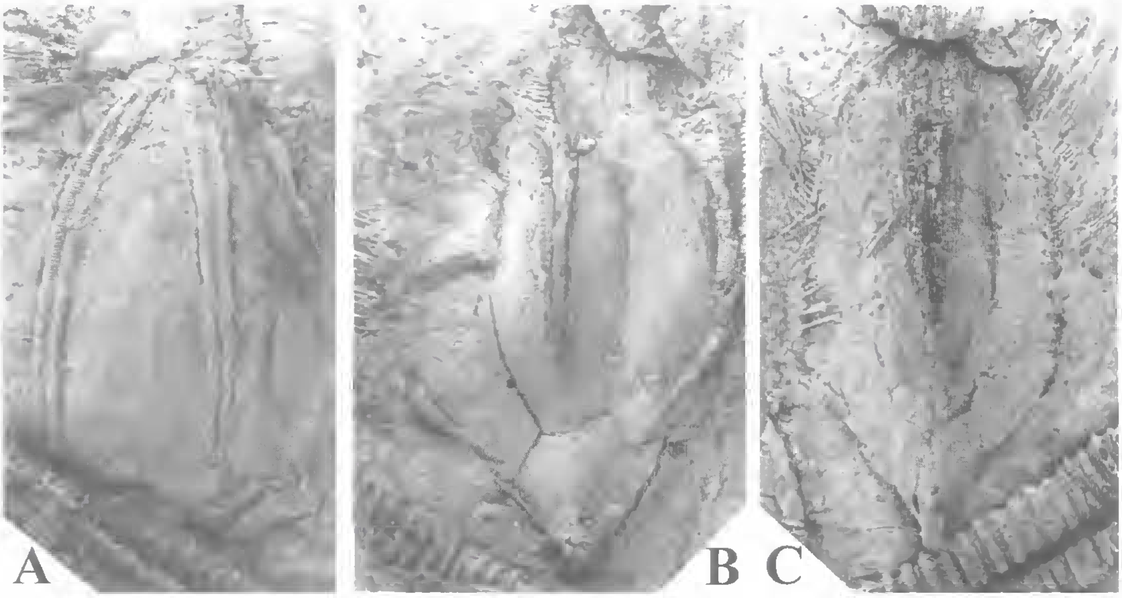


FIG. 59. *Pachyblastus dicki* Breimer & Macurda, 1972, all latex casts from external moulds of blastoid thecae in lateral view, all on one slab SAM K1068 ×2. A, holotype.

DESCRIPTION. Free arm fragments only available. Dorsal aspect with 2 columns of ambulacrals alternating along slightly zigzag arm axis and 2 lateral columns of club-shaped adambulacrals; ambulacrals closely sutured to each other within the column and across the arm axis, wider than long, smooth, weakly convex dorsal surface, with protruding obtusely angular adradial margin and concave abradial margin; adambulacrals dorsally separated from ambulacrals by short distance (ad-ab) less than the width of ambulacrals in which are discernible circular holes at the concave abradial margin, subquadrate, dorsally convex, about 1/2 width of adjacent ambulacral.

Ventral aspect with discrete narrow ambulacral channel and wide shallow ambulacral groove; ambulacrals boot-shaped, with attenuated toe sutured to opposing adradial projection on adambulacral; adambulacral greatly expanded abradially, not obviously bearing any spines; podial basins small in relation to size of surrounding plates, shared by 2 succeeding ambulacrals and adjacent adambulacrals.

REMARKS. This arm structure is distinguished among the South African ophiuroids described here by the close suture rather than a cleft between successive ambulacrals dorsally. Only *Haughtonaster reedi* Rilett, 1971 is comparable in this respect but its adambulacrals are distinctly different both dorsally and ventrally. We are not aware of a comparable arm structure in any known ophiuroid but with the preservation of this specimen we are forced to retain it in open nomenclature.

Ophiuroid arms indet. C
(Fig. 58D, E)

MATERIAL. B4560 from Gydo Pass (C2S1) and RO745 from Gamkapoort 33° 18'S, 21° 38'E (C2S1).

DESCRIPTION. Incomplete and partly disarticulated arm fragments only.

Dorsal. Ambulacrals in 2 columns, alternating along arm axis, about twice as wide as long, closely sutured (without cleft) along column and to opposing column, smooth; adambulacrals not evident dorsally.

Ventral. Ambulacral channel narrow, deep. Ambulacrals with strong boot-shaped ridge having thick leg, with pit in the floor of podial basin into abradial side of ambulacral. Adambulacral with L-shaped ridge abutting against toe of ambulacral and of more or less uniform width or wider in lateral longitudinal part, bearing numerous short pointed lateral spines. Podial basin with small perforation through floor between ambulacral and adambulacral, shared on 2 ambulacrals and one adambulacral, wider than long.

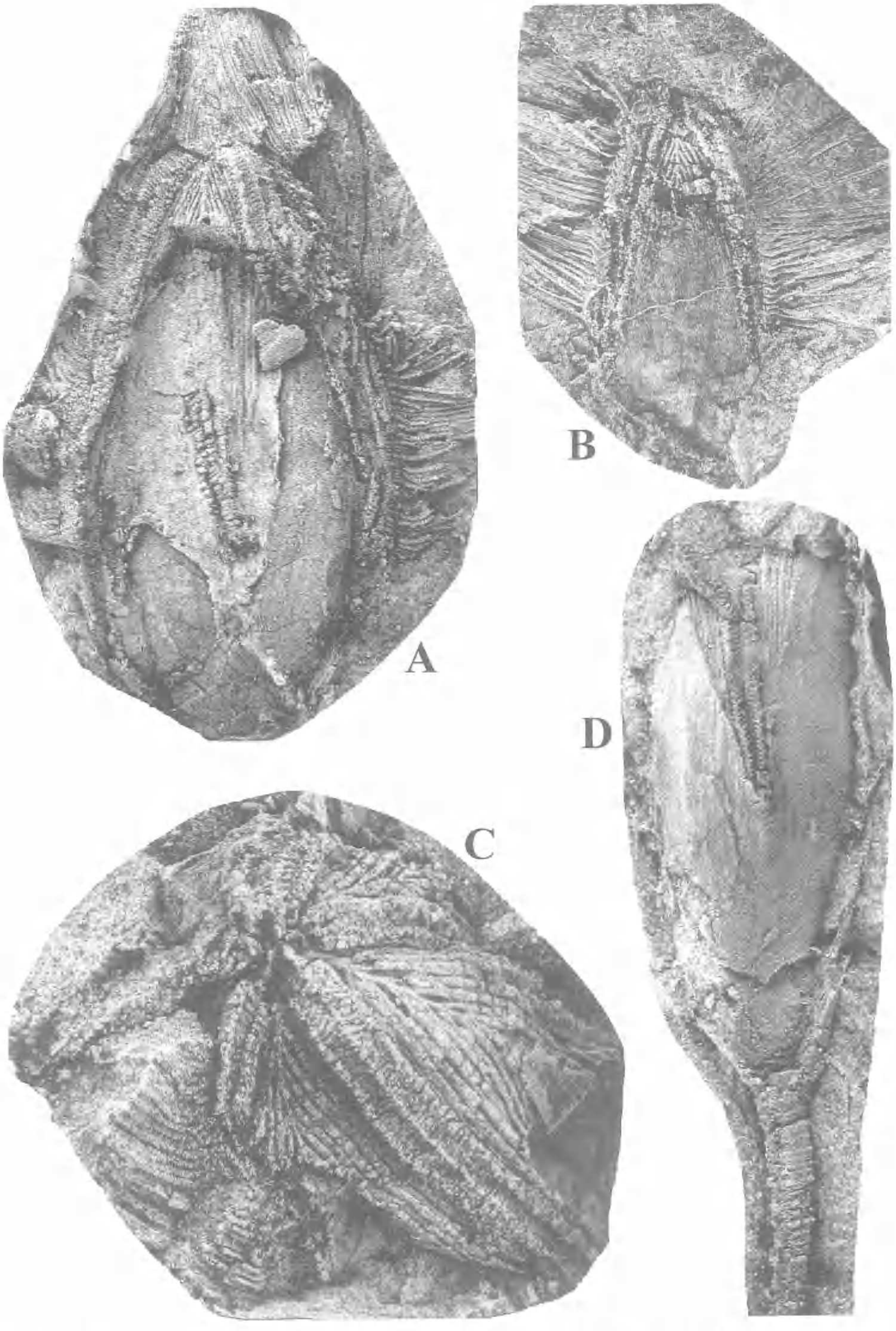


FIG. 60. *Pachyblastus dicki* Breimer & Macurda, 1972. A, lateral view of latex cast from part internal and part external (adorally) mould, B4590 ×2.2. B, lateral view of incomplete theca B4580 ×2.2. C, oblique dorsal view of theca B4597 ×2.7. D, lateral view of theca and proximal stem B4589 ×2.2.

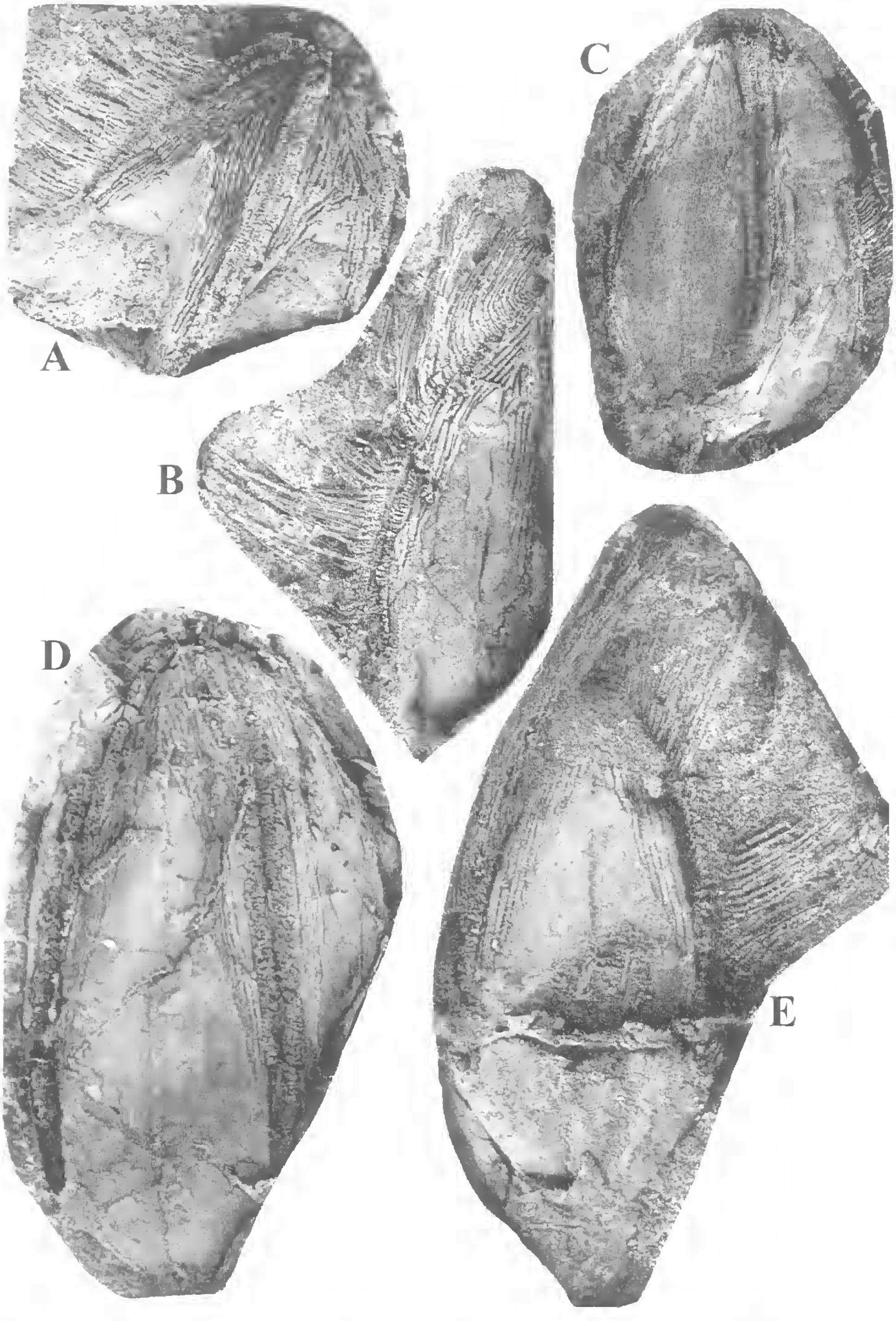


FIG. 61. *Pachyblastus dicki* Breimer & Macurda, 1972. A, oblique lateral view of incomplete theca B4597 ×2. B, lateral view of incomplete theca bearing long brachioles B4584 ×2. C, lateral view of theca B4521 ×1.7. D, lateral view of incomplete theca RO34a ×2.5. E, lateral view of theca with long brachioles in place and oral end missing B4570 ×2.5.

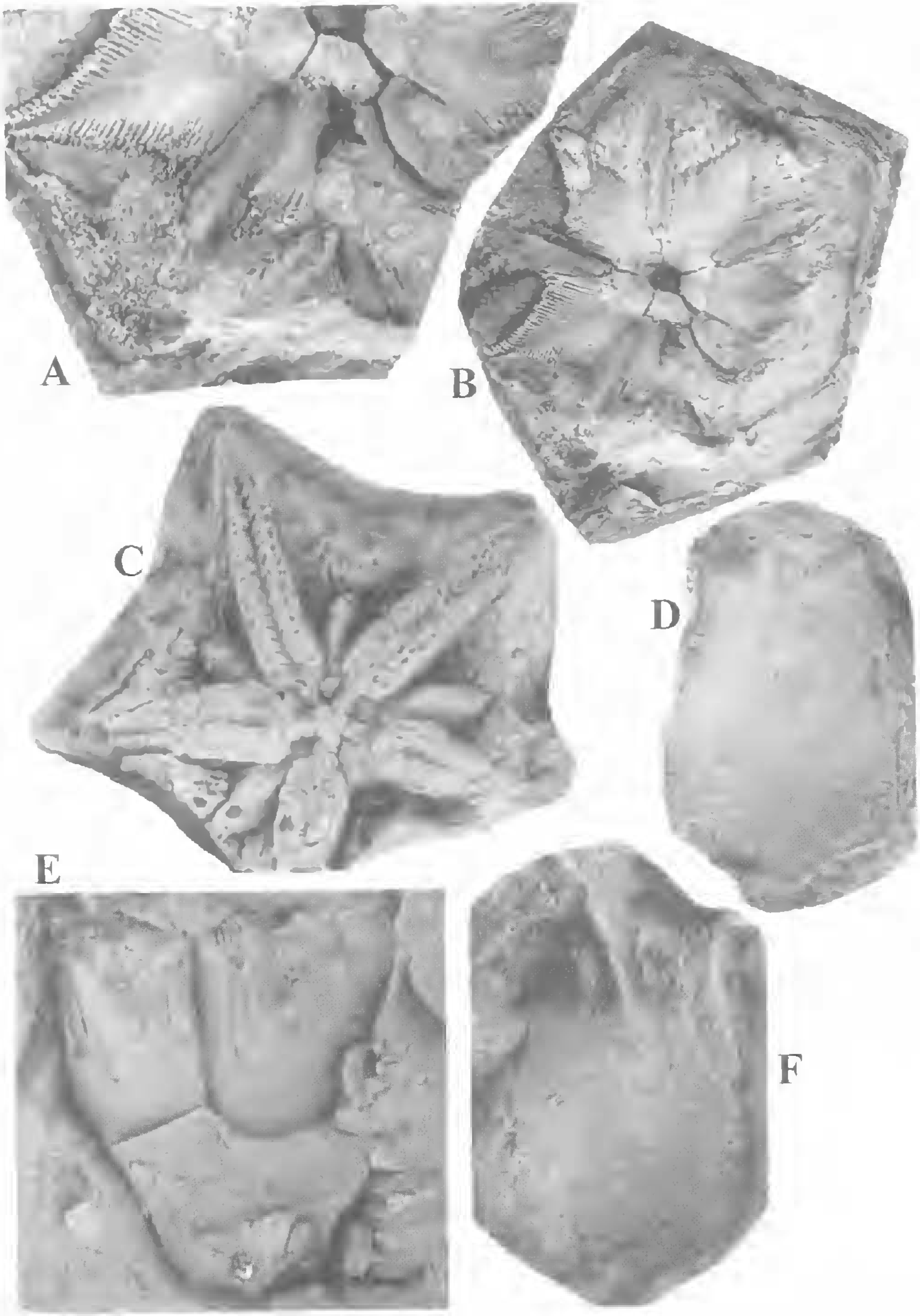


FIG. 62. *Brachyschisma oostheizeni* Breimer & Macurda, 1972. A, B, interior view of oral surface of theca B4597 ×3.4 an ×1.7, respectively. Anal opening at 6 o'clock. C, oral view of holotype, a juvenile RO35(5) ×6. D, interior view of latex cast of radial SM A3045 ×5.2. E, lateral view of latex cast from juvenile theca RO 732(1) ×3.4. F, interior view of latex cast of radial RO F10 ×5.2.

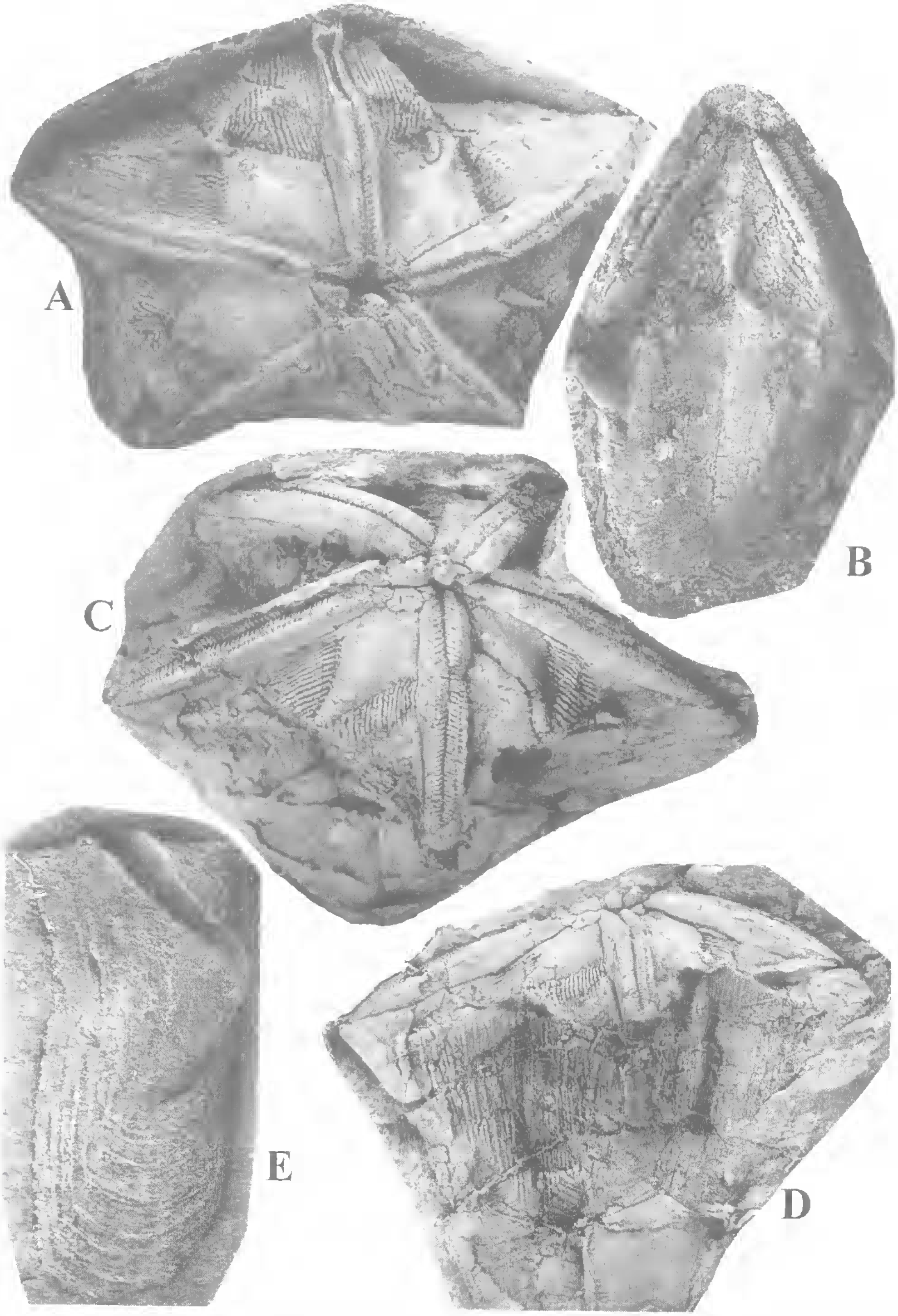


FIG. 63. *Brachyschisma oostheizeni* Breimer & Macurda, 1972. A, oral view of latex cast of theca with anal interarea at 6 o'clock B4596 ×2.5. B, lateral interradial view of latex cast of B4540 ×3.4. C,D, oblique oral and lateral views, respectively, of crushed B4595 ×2.5. E, lateral view of exterior of radial RO 35(6) ×2.5.

REMARKS. These poorly preserved specimens do not provide sufficient detail for identification but the wide ambulacrals and style of adambulacrals suggest affinity with the Cheiropterasteridae and the specimens could belong to *Hexuraster weitzi* Spencer, 1950a but we prefer to retain them in open nomenclature given their poor state of preservation.

Class BLASTOIDEA Say, 1825
Order FISSICULATA Jaekel, 1918
Family NYMPHAEOBLASTIDAE Wanner, 1940

Pachyblastus Breimer & Macurda, 1972

TYPE SPECIES. *Pachyblastus dicki* Breimer & Macurda, 1972.

Pachyblastus dicki Breimer & Macurda, 1972
(Figs 59-61)

MATERIAL. HOLOTYPE: SAMK1068 from the road from Hex Rivier Pass to Montagu Koo, 14km S of turnoff from N9, E of DeDooms. B4519 from Theronsberg Pass near Ceres in the Waboomberg Formation, B4521, B4522 from Matroosberg, Stinkfontein (Hex River Pass). B4570, B4580, B4584, B4590 from the type locality. RO34a from Matroosberg, Worcester (Hex River Pass). 33°30'S, 19°49'E.

REMARKS. Breimer & Macurda (1972) and Macurda (1979, 1983) provided detailed descriptions of this monotypic genus based on the type material from South Africa and on Bolivian material of similar age in the Emsian. Breimer & Macurda (1972) noted that the type material, collected by Mr R.I. Dick was at that time in his private collection. In 1993 Mr Dick donated his collection to the Geological Survey of South Africa and it is now catalogued at the Regional Office at Bellville. Breimer & Macurda (1972) figured only 3 specimens on the type slab; this is a large slab and has many more specimens exposed on it, all as moulds. In this paper we have illustrated 3 latex casts (Fig. 59) from the moulds illustrated by Breimer & Macurda (1972) as well as latex casts of other individuals from the type and other slabs. These provide a more complete picture of the species but on no one of them are the anal deltoid plates clearly exposed.

The South African specimens figured herein differ from the Bolivian specimens (Macurda, 1979) by: 1, the very narrow median deltoid crest with hydrospire slits right up to the crest as opposed to a broader median zone without slits and bearing a broad low crest; 2, the side plates on the ambulacra concealing the lancet completely up to the adoral end; 3, a narrow ridge extending adorally from the adoral end of each ambulacrum (Fig. 60C) which may be due to preservation with the mouth closed. However, we would not suggest that these differences are sufficient to erect a new species and retain Macurda's concept of the species.

Family OROPHOCRINIDAE Jaekel, 1918

Brachyschisma Reimann, 1945

TYPE SPECIES. *Codaster corrugatus* Reimann, 1935 from the Middle Devonian of New York; by original designation.

Brachyschisma oostheizeni
Breimer & Macurda, 1972
(Figs 62, 63)

MATERIAL. HOLOTYPE: RO35 (Breimer & Macurda, 1972, pl. 6, fig. 3) from Gamkaskloof, Prince Albert (33°20'45"S, 21°47'30"E (C2S1). SMA3045 (Breimer & Macurda, 1972, pl. 6, fig. 13) from a road cutting between De Doorns and Triangle (Hex River Pass). RO732 (Breimer & Macurda, 1972, pl. 6, fig. 10), RO734 from Gamkapoort, Prince Albert, 33°18'S, 21°38'E (C2S1). ROE10 from Damascus, Prince Albert, 33°17'15"S, 21°55'45"E (C2S1). B4540 from Hex River Pass (C2S1). B4595, 4596 from Gydo Pass and Vleiland (C2S1), respectively. SAM13463, SAMK1026 from Koudeveldberg. SAM3376 from Laken Vlei, Ceres (C2S1).

DESCRIPTION. The following descriptive notes are additional to the accurate and detailed description of Macurda (1983: 80-81) or reflect the availability of much larger individuals and thus indications of changes with growth. Deltoid median radial crest most prominent in juveniles (e.g. holotype), becoming lower and broader relative to plate size with growth, higher distally at oral end of RR suture. Macurda (1983:81) gave measurements of a deltoid from the holotype whereas the following measurements are from a large specimen (Fig. 63A): L.: 10mm; Gr.Ad.W.: 1.2mm; Min.W.: 1.2mm; Gr.Ab.W.: 3.8mm; Deltoid lip 1/5 as long as deltoid body. Small specimens with 5-8 hydrospires per group whereas large specimens have up to 19 per group.

Anal deltoids 3, super-, sub- and hypodeltoid. Superdeltoid bordering oral opening, extending distally to tips of lancets, widest distally. Anal opening elliptical, elongate in radial direction. Subdeltoid horseshoe-shaped around proximal part of anal opening, with unequal limbs on either side of anal opening; with limb on D side shorter and narrower than that on C side, lacking hydrospires and not reaching radial but rather abutting hypodeltoid; with limb on C side abutting radial and sharing with it a greatly reduced (for a large specimen) group of 6-8 hydrospires. Hypodeltoid disarticulated and not available on the latex (Fig. 62A) but space left by it approximately pentagonal and forming distal margin of anal opening (this margin is thus uncertain).

Hydrospire groups 9, absent from D side of anal interarea but present on C side.

REMARKS. The description given by Breimer & Macurda (1972) and Macurda (1983) was detailed and valid and is not repeated herein. Macurda (1983: 81) remarked that generic assignment could not be definite without knowledge of the anal deltoids. The anal deltoids are clear on the internal mould figured herein (Fig. 62A, B) and confirm the assignment to *Brachyschisma* while the larger specimens dealt with herein agree with Macurda's (1983) observation that *Brachyschisma* is the only comparable Devonian blastoid.

ACKNOWLEDGEMENTS

We are grateful to Roy Oosthuizen for allowing us to describe material from his private collection which is destined for the South African Museum; Norton Hiller, then of Rhodes University, Grahamstown who provided material in his care; John Almond, Geological Survey of South Africa, Bellville for extensive curatorial assistance; Roy Dick for donation of material, Bianca Lawrence of the Natal Museum for loan of Rilett's types; Colin McCrae, Geological Survey of South Africa, Pretoria for access to collections in his care; Paul Avern, Queensland Museum for extensive photographic assistance; the Director of the South African Museum for access to collections and the 2 reviewers for valuable suggestions. PAJ is particularly thankful to the Australian Department of Industry, Technology and Commerce for a Bilateral Science and Technology Grant without which this project would not have been possible.

LITERATURE CITED

AUSICH, W.I. 1986. Early Silurian Rhodocrinitacean crinoids (Brassfield Formation, Ohio). Journal of Paleontology 60: 84-106.

1987. Brassfield Compsocrinina (Lower Silurian crinoids) from Ohio. Journal of Paleontology 61: 552-562.

BATHER, F.A. 1890. British fossil crinoids. II. The classification of the Inadunata Fistulata (cont'd). Annals and Magazine of Natural History, series 6, 5: 373-388.

BECKER, G., BLESS, J.M. & THERON, J.N. 1994. Malvinokaffric ostracods from South Africa (Southern Cape: Bokkeveld Group, Devonian). Courier Forschungs-Institut Senckenberg 169: 239-259.

BILLINGS, E. 1858. On the Asteriadae of the Lower Silurian rocks of Canada. Geological Survey of Canada, Figures and Descriptions of Canadian Organic Remains, decade 3: 75-85.

BJORK, P.R., GOLDBERG, P.S. & KESLING, R.V. 1968. Mouth frame of the ophiuroid *Onychaster*. Contributions from the Museum of Paleontology, University of Michigan 22: 45-60.

BLAKE, D.B. & GUENSBURG, T.E. 1989. Two new multiarmed Paleozoic (Mississippian) asterids (Echinodermata) and some paleobiologic implications. Journal of Paleontology 63: 331-340.

BOUCOT, A.J. 1971. Malvinokaffric Devonian marine community distribution and implications for Gondwana. Anais da Academia Brasileira de Ciencias 43 (supplement): 23-49.

BOUCOT, A.J., JOHNSON, J.G. & TALENT, J.A. 1969. Early Devonian brachiopod zoogeography. Special Papers of the Geological Society of America 119: 1-106.

BREIMER, A. 1962. A monograph on Spanish Palaeozoic Crinoidea. Overdruk uit Leidse Geologische Mededelingen 27: 1-189.

BREIMER, A. & MACURDA, D.B. 1972. The phylogeny of the fissiculate blastoids. Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afd. Natuurkunde, Eerste Reeks 26(3): 1-390.

BRONN, H.G. 1848. Index palaeontologicus oder Ubersicht der bis jetztbekannten fossilen Organismen, unter Mitwirkung der Herren Professor H.R. Göppert und H. von Meyer: Handbuch einer Geschichteder Natur 3, Abt. 1 (1,2), part 3, A. Nomenclator palaeontologicus. 1381p. (Schweizerbart: Stuttgart).

CLARKE, J.M. 1913. Fosseis devonianos do Paraná. Monographias do Servico Geologico e Mineralogico do Brasil 1: 1-353.

CORSTORPHINE, G.S. 1897. Report of the Acting Geologist for the year 1897. Report of the Geological Commission of the Cape of Good Hope 1897: 3-43.

DONOVAN, S.K. & CLARK, N.D.L. 1992. An unusual crinoid columnal morphospecies from the Llandovery of Scotland and Wales. Palaeontology 35: 27-35.

FOLLMANN, O. 1887. Unterdevonische Crinoiden. Verhandlungen des Naturhistorischen Vereines der preussischen Rheinlande, Westfalens und des Reg.-Bezirks Osnabrück 44: 113-138.

FREST, T.J. & STRIMPLE, H.L. 1981. New camerate crinoids from the Silurian of North America. Journal of Paleontology 55:639-655.

GOLDFUSS, G.A. 1848. Ein Seestern aus der Grauwacke. Verhandlungen des naturhistorischen Vereines der preussischen Rheinlande 5: 145-146, 5pl.

GOLDRING, W. 1923. The Devonian crinoids of the State of New York. Memoirs of the New York State Museum 16: 1-670.

1954. Devonian crinoids: new and old, II. New York State Museum Circular 37: 1-51.

HAECKEL, E.H. 1866. Allgemeine Entwickelungsgeschichte der Organismen. In Haeckel, E. General Morphologie der Organismen. Vol. 2. 160p. (Berlin).

HALL, J. 1858. Report of the Geological Survey of Iowa, embracing the results of investigations made during portions of the years 1855, 1856, and 1857. Palaeontology of Iowa 1(2): 473-724. (Geological Survey of Iowa).

1879. The fauna of the Niagara Group in central Indiana. Annual Report of the New York State Museum of Natural History 28: 99-199.

HARPER, J.A. 1985. A new look at *Eugasterella logani* (Hall, 1868) (Stellaroidea:Ophiuroidea) from the Middle Devonian of New York State. Annals of the Carnegie Museum 54: 357-373.

HAUDE, R. 1995. Lower Devonian echinoderms from the Precordillera (Argentina). Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 197: 37-86.

1999. Der - verzögerte - Ersatz eines Homonyms: *Marginaster* Haude, 1995. Neues Jahrbuch für Geologie and Paläontologie Monatschefte 1999: 3p.

HILLER, N. & THERON, J.N. 1988. Benthic communities in the South African Devonian. Canadian Society of Petroleum Geologists Memoir 14: 229-242.

HINDE, G.J. 1885. Description of a new species of crinoids with articulating spines. Annals and Magazine of Natural History, series 5, 15: 157-173.

HOTCHKISS, F.H.C. 1970. North American Ordovician Ophiuroidea, the genus *Taeniaster* Billings, 1858 (Protasteridae). Proceedings of the Biological Society of Washington 83: 59-76.

1976. Devonian ophiuroids from New York State: reclassification of *Klasmura*, *Antiquaster*, and *Stenaster* into the suborder Scalarina nov., Order Stenurida. Bulletins of the New York State Museum 425: 1-39.

1993. A new Devonian ophiuroid (Echinodermata: Oegophiurida) from New York State and its bearing on the origin of ophiuroid upper arm plates. Proceedings of the Biological Society of Washington 106: 63-84.

1995. Loven's Law and adult ray homologies in echinoids, ophiuroids, edrioasteroids, and an ophiocistioid (Echinodermata: Eleutherozoa). Proceedings of the Biological Society of Washington 108: 401-435.

JAEKEL, O. 1918. Phylogenie und System der Pelmatozoen. Paläontologische Zeitschrift 3(1): 1-128.

JELL, P.A. 1997. Early Carboniferous ophiuroids from Crawfordsville, Indiana. Journal of Paleontology 71: 306-316.

1999. Silurian and Devonian crinoids from central Victoria. Memoirs of the Queensland Museum 43: 1-114.

KESLING, R.V. 1972. *Strataster devonicus*, a new brittle-star with unusual preservation from the Middle Devonian Silica Formation of Ohio. Contributions from the Museum of Paleontology, University of Michigan 24: 9-15.

KESLING, R.V. & LE VASSEUR, D. 1971. *Strataster ohioensis*, a new early Mississippian brittle-star, and the paleoecology of its community. Contributions from the Museum of Paleontology, University of Michigan 23: 305-341.

KESLING, R.V. & CHILMAN, R.B., 1975. Strata and megafossils of the Middle Devonian Silica Formation. Papers in Paleontology from the Museum of Paleontology, University of Michigan 8: 5-123, 153-172.

KIER, P.M., 1952. Echinoderms of the Middle Devonian Silica Formation of Ohio. Contributions from the Museum of Paleontology, University of Michigan 10: 59-81.

1958. Infrabasals in the crinoid *Opsiocrinus* Kier. Contributions from the Museum of Paleontology, University of Michigan 13: 201- 206.

KIRK, E. 1934. *Corynecrinus*, a new Devonian crinoid genus. Proceedings of the U.S. National Museum 83(2972): 1-7.

KNOD, R. 1908. Devonische Faunen Boliviens. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beil. Band 25: 493-600.

KOZLOWSKI, R. 1923. Faune dévonienne de Bolivie. Annales de Paléontologié 12: 1-112.

LEHMANN, W.M. 1957. Die Asterozoen in den Dachschiefern des rheinischen Unterdevons. Abhandlungen des Hessischen Landesamtes für Bodenforschung 21: 1-160, 55 pls.

LYON, S.S. 1857. Palaeontological Report. Geological Report of Kentucky 3: 467-497.

MACURDA, D.B. 1979. The Devonian blastoids of Bolivia. Journal of Paleontology 53: 1361-1373.

1983. Systematics of the fissiculate Blastoidea. Papers in Paleontology from the Museum of Paleontology at the University of Michigan 22: 1-291.

McINTOSH, G.C. 1979. Abnormal specimens of the Middle Devonian crinoid *Bactrocrinites* and their effect on the taxonomy of the genus. Journal of Paleontology 53: 18-28.

1983. Review of the Devonian cladid inadunate crinoids: Suborder Dendrocrinina. PhD Thesis, University of Michigan.

1986. Phylogeny of the dicyclic inadunate crinoid Order Cladida. Abstr. 4th North American Palaeontological Convention.

McINTOSH, G.C. & BRETT, C.E., 1988. Occurrence of the cladid inadunate crinoid *Thalamocrinus* in the Silurian (Wenlockian) of New York and Ontario. Contributions to the Life Sciences from the Royal Ontario Museum 149: 1-17.

MILLER, S.A. 1889. North American geology and paleontology. (Western Methodist Book Concern: Cincinnati).

MILLER, S.A. & GURLEY, W.F.E. 1895. Description of new species of Palaeozoic Echinodermata. Illinois State Museum Bulletin 6: 1-62.

MOORE, R.C. 1962. Ray structures of some inadunate crinoids. University of Kansas, Paleontological Contributions, Echinodermata, Article 5: 1-47.

MOORE, R.C. & JEFFORDS, R.W., 1968. Classification and nomenclature of fossil crinoids based on studies of their columns. University of Kansas, Paleontological Contributions, Echinodermata, Article 9(46): 1-86.

MOORE, R.C., LANE, N.G. & STRIMPLE, H.L., 1978. Order Cladida Moore & Laudon, 1943. Pp. T578-T759. In Moore, R.C. & Teichert, C. (eds) Treatise on invertebrate paleontology, Part T, Echinodermata 2 (Geological Society of America & University of Kansas Press: Boulder, Colorado & Lawrence, Kansas).

MOORE, R.C. & LAUDON, L.R., 1943. Evolution and classification of Paleozoic crinoids. Geological Society of America Special Paper 46: 1-153.

MOORE, R.C. & TEICHERT, C. (eds) 1978. Treatise on invertebrate paleontology, Part T, Echinodermata 2, Crinoidea. 3 vols. (Geological Society of America & University of Kansas Press: Boulder, Colorado & Lawrence, Kansas).

OOSTHUIZEN, R.D.F. 1984. Preliminary catalogue and report on the biostratigraphy and palaeogeographic distribution of the Bokkeveld fauna. Transactions of the Geological Society of South Africa 87: 125-140.

PERRIER, E. 1881. Description sommaire des espèces nouvelles d'astérias. Bulletin of the Museum of Comparative Zoology, Harvard University 9: 1-31.

REED, F.R.C. 1904. Mollusca from the Bokkeveld Beds. Annals of the South African Museum 4: 239-274.

1906. New fossils from the Bokkeveld Beds. Geological Magazine, Decade 5, 3: 301-310.

1907. Fauna of the Bokkeveld beds. Geological Magazine, Decade 5, 4: 166-171, 222-232.

1925. Revision of the fauna of the Bokkeveld Beds. Annals of the South African Museum 22: 27-225.

REIMANN, I.G. 1935. New species and some new occurrences of Middle Devonian blastoids. Bulletin of the Buffalo Society of Natural History 17: 23-45.

1945. New Devonian blastoids. Bulletin of the Buffalo Society of Natural Sciences 19(2): 22-42.

RENNIE, J.V.L. 1936. On *Placocystella*, a new genus of cystids from the Lower Devonian of South Africa. Annals of the South African Museum 31: 269-275.

RILETT, M.H.P. 1971. Two new fossil ophiuroid species from the Bokkeveld Series, near Ceres, Cape Province. Annales of the Natal Museum 21: 29-35.

ROEMER, F. 1863. Neue Asteriden und Crinoiden aus devonischem Dachschiefer von Bundenbach bei Birkenfeld. Palaeontographica 9:143-152, pls 23-29.

ROSSOUW, P.J., 1933. On the geology of Weltevreden, Prince Albert district, with a diagnosis of an ophiuroid, *Ophiurites* sp. Transactions of the Geological Society of South Africa 36: 73-76.

RUEDEMANN, R. 1916. Palaeontologic contributions from the New York State Museum. New York State Museum Bulletin 189: 1-225.

RUST, I.C. 1973. The evolution of the Palaeozoic Cape Basin, southern margin of Africa. Pp. 247-276. In Nairn, A.E.M. & Stehli, F.G. (eds) The ocean basins and margins, 1. The South Atlantic. (Plenum: New York).

RUTA, M. & THERON, J.N. 1997. Two Devonian mitrates from South Africa. Palaeontology 40: 201-243.

SALTER, J.W. 1856. Description of Palaeozoic Crustacea and Radiata from South Africa. Transactions of the Geological Society of London 7: 215-224.

SANDBERGER, F. 1852. Über einige paläozoische Versteinerungen des Cap-Landes. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefactin-Kunde, Abhandlungen A 1852: 581-585.

SCHMIDT, W.E. 1934. Die Crinoideen des Rheinischen Devons. Teil I: Die Crinoideen des Hunsrückschiefers. Abhandlungen der Preussischen Geologischen Landesanstalt 163: 1-149.

1941. Die Crinoideen des Rheinischen Devons. Abhandlungen der Reichsstelle für Bodenforschung, Neue Folge 182: 1-253, pls 1-26.

SCHÖNDORF,F. 1910. Paläozoische Seesterne Deutschlands. 2. Die Aspidosomatiden des deutschen Unterdevon. Palaeontographica 57: 1-66.

SCHUCHERT, C. 1914. Stellaroidea palaeozoica. Pp.1-53. In Frech, F. (ed.) Fossilium Catalogus 1: Animalia Part 3. (W. Junk: Berlin).

1915. Revision of Paleozoic Stelleroidea with special reference to North American Asteroidea. United States National Museum Bulletin 88:1-311, pls 1-38.

SCHWARZ, E.H.L. 1906. South African Palaeozoic fossils. Records of the Albany Museum 1: 347-404.

SHARPE, D. & SALTER, J.W. 1856. Description of Palaeozoic fossils from South Africa. Transactions of the Geological Society of London 7: 203-206.

SIMON, E. 1884. Note sur le groupe des *Microbothria*. Bulletin de la Societé du Zoologique 9: 313-317.

SMITH, A.B. & JELL, P.A. 1990. Cambrian edrioasteroids from Australia and the origin of starfishes. Memoirs of the Queensland Museum 28: 715-778.

SPENCER, W.K., 1914. British Palaeozoic Asterozoa. Part 1. Palaeontographical Society Monographs 1913: 1-56

1930. British Palaeozoic Asterozoa. Part 8. Palaeontographical Society Monographs 1928: 389-436.

1934. British Palaeozoic Asterozoa. Part 9. Palaeontographical Society Monographs 1933: 437-494.

1950a. A new brittlestar and an eurypterid from the Bokkeveld Strata. South African Journal of Science 46: 300-301.

1950b. Asterozoa and the study of Palaeozoic faunas. Geological Magazine 87:393-408.

SPENCER, W.K. & WRIGHT, C.W. 1966. Asterozoans. Pp. U4-U107. In Moore, R.C. (ed.). Treatise on invertebrate paleontology. Part U. Echinodermata 3(1). (Geological Society of America & University of Kansas Press: New York).

STEWART, G.A., 1940. Crinoids from the Silica Shale, Devonian, of Ohio. Ohio Journal of Science 40: 53-61.

STUKALINA, G.A., 1978. Cystoidea and crinoids. Trudy Institut Geologii i Geofiziki 397: 145-164.

TANKARD, A.J. & BARWIS, J.H. 1982. Wave-dominated deltaic sedimentation in the Devonian Bokkeveld basin of South Africa. Journal of Sedimentary Petrology 52: 959-974.

THERON, J.N. 1970. A stratigraphical study of the Bokkeveld Group (Series). Pp. 197-204. In Haughton, E.H. (ed.) Second International Gondwana Symposium, Proceedings and Papers (Council for Scientific and Industrial Research: Pretoria).

1972. The stratigraphy and sedimentation of the Bokkeveld Group. DSc Thesis, University of Stellenbosch.

THERON, J.N. & JOHNSON, M.R. 1991. Bokkeveld Group (including the Ceres, Bidouw and Traka Subgroups). Pp. 3-3 to 3-6. In Johnson, M.R. (ed.) Catalogue of South African Lithostratigraphic units. (South African Committee for Stratigraphy: Pretoria).

THERON, J.N. & LOOCK, J.C. 1988. Devonian deltas of the Cape Supergroup, South Africa. Canadian Society of Petroleum Geologists Memoir 14: 729-740.

THERON, J.N., BASSON, W.A. & HILL, R.S. 1995. Lithostratigraphy of the Gamka Formation (Bokkeveld Group). Lithostratigraphic series, South African Committee for Stratigraphy 29: 1-13.

THOM, G. 1830. Remarks on the geology of South Africa. South African Quarterly Journal 1: 269-271.

UBAGHS, G. 1978. Camerata. Pp. T408-T519. In Moore, R.C. & Teichert, C. (eds) Treatise on invertebrate paleontology, Part T, Echinodermata 2, Crinoidea. (Geological Society of America & University of Kansas Press: Boulder, Colorado & Lawrence, Kansas).

WACHSMUTH, C. & SPRINGER, F. 1880. Revision of the Palaeocrinoidea. Part 1, the families Ichthyocrinidae and Cyathocrinidae. Proceedings of the Academy of Natural Sciences of Philadelphia 1880: 226-378.

1886. Revision of the Palaeocrinoidea. Part 3, Section 2. Discussion of the classification and relations of the brachiate crinoids, and conclusion of the generic descriptions. Proceedings of the Academy of Natural Sciences of Philadelphia 1886: 64-226.

1897. The North American Crinoidea Camerata. Harvard College Museum of Comparative Zoology Memoir 20: 1-897, pls 1-83 (3 vols).

WANNER, J. 1940. Neue Blastoideen aus dem Perm von Timor (mit einem Beitrag zur Systematik der Blastoideen). Geological Expedition to the Lesser Sunda Islands under the leadership of H.A. Brouwer 1: 217-277.

WILLIAMS, H.S. 1883. On a crinoid with movable spines (*Arthroacantha ithacensis*). American Philosophical Society Proceedings 21: 81-88.

WITHERS, R.B. & KEBLE, R.A. 1934. The Palaeozoic starfish of Victoria. Proceedings of the Royal Society of Victoria, new series 46: 220-249.